ECOLOGICAL STUDIES IN THE INDIGENOUS FORESTS OF NORTH WESTLAND, NEW ZEALAND

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ABSTRACT

The geographical limits of the four Nothofagus species in north Westland are described. An examination is made of the stability of the existing beech forest boundary and of factors which may limit the expansion of the boundary. Recent rates of migration on different growing sites are estimated. The slowest rate of migration, 0.1 m/yr, occurs on hill slopes. More rapid migration is possible along flood plains, across poorly-drained high terraces and in the upland zone of the southern Paparoa Range. Nothofagus migration appears to proceed largely by slow marginal spread from existing stands and occasionally, by the formation of outliers following the long-distance dispersal of seed over distances of up to 12 km. It is proposed that the Nothofagus species have spread slowly throughout the past 10 000 years from nine, local glacial-period refugia and that there are no barriers to further expansion into central Westland.

The population structures and regeneration requirements of the seven major canopy tree species of the lowland forests in north Westland are compared. The species studied were Dacrydium cupressinum, Podocarpus ferrugineus, Metrosideros umbellata, Quintinia acutifolia, Weinmannia racemosa, Nothofagus truncata and N. fusca. Seedling establishment, growth and mortality were studied using permanent quadrats and tagged populations over a three year period.

A deficiency of large seedlings, saplings, poles and small canopy trees is evident in D. cupressinum, P. ferrugineus, M. umbellata and, to a lesser extent,

N. fusca populations. For *D. cupressinum* the rate of regeneration appears to have declined from the period 400-500 years ago up till about 100 years ago when an upsurge in regeneration began. This parallels in extent and timing a regeneration decline in *P. ferrugineus* but predates a decline in *M. umbellata* and *N. fusca*. It is postulated that long-term changes in regeneration rates resulted from catastrophic damage to the hardwood component of the forest canopy within the period 300-500 years ago.

CONVENTIONS:

(i) Plant nomenclature follows Allan (1961) and Philipson (1965)

(ii) Standard metric system (SI) symbols are used throughout.

(iii) Statistical tests follow Sokal and Rohlf (1969).

(iv) The following abbreviations are commonly used:

a.s.l. = above sea level

d.b.h. = diameter at breast height

(v) Radiocarbon dates are based on a C^{14} half-life of 5 568 yrs (Dates for key sites based on a half-life of 5 730 yrs and corrected for secular effects are shown in Appendix III).

TERMS USED:

(i) The word 'symbiosis' is used in its broader sense, referring to intimate and often obligatory associations of two species which can be parasitic or mutualistic. (c.f. Ricklefs, 1973; Keeton 1980).

(ii) The distinction between 'upland' and 'lowland' forests is based on the upper altitudal limits of major canopy tree species. In the study area, this limit is c 700m a.s.l. and is based on the upper altitudinal limits of hard beech, rimu, miro and *Quintinia acutifolia* (Kirkland and Trotman, 1974; Franklin and Nicholls, 1974). Wardle's definition (Wardle, 1964) is used for the term 'subalpine'.

(iii) Commonly used plant names, with scientific equivalents are as follows:

hard beech	*Nothofagus truncata*
kamahi	*Weinmannia racemosa*
miro	*Podocarpus ferrugineus*
mountain beech	*Nothofagus solandri* var. *cliffortioides*
Quintinia	*Quintinia acutifolia*
rata (southern rata)	*Metrosideros umbellata*
red beech	*Nothofagus fusca*
rimu	*Dacrydium cupressinum*
silver beech	*Nothofagus menziesii*

(iv) In relation to *Nothofagus* distributions, the term 'outlier' is used to describe individuals or stands isolated from

the main area of distribution. The term applies to individuals and stands located within or surrounded by communities lacking *Nothofagus* and also to individuals and stands located within or surrounded by *Nothofagus* forest lacking the species comprising the outlier. Individuals and stands located more than 30 m from the main area of distribution are regarded as outliers. This distance is beyond the normal range of seedling establishment along the margins of existing *Nothofagus* stands (see sections 4.4 and 4.6).

CHAPTER ONE

INTRODUCTION AND AIMS

The indigenous vegetation of New Zealand has a number of features which seem to indicate instability in the spatial distribution of species, and in community and population structures. Many of these features were first described by one of the earliest New Zealand plant ecologists, Leonard Cockayne (1855-1934), and have subsequently been the subject of much ecological research in the country.

The most striking of these features, which are the subject of this study, are the large discontinuities in the distribution of *Nothofagus* (see Figs 1 & 2), the signs of an expansion of the *Nothofagus* range by the invasion of adjoining vegetation, and the apparent regeneration failure over wide areas of some gymnosperm species. There is also evidence in different parts of New Zealand of a lowering of timberline and the upper altitudinal limits of tree species (Holloway, 1954; Elder, 1963; McKelvey, 1963) and the invasion of open bogs by the marginal forest (Holloway, 1954). The occurrence of surface logs, buried wood and charcoal, buried podsols and windthrow dimples on the ground surface throughout the eastern South Island provides evidence for the widespread destruction of forest by fire in the past and the consequent replacement of forest by tussock grassland and scrubland (Raeside, 1948; Holloway, 1954; Molloy *et al.*, 1963). Subsequent reinvasion of grassland and scrubland by forest is a gradual and localised process (Wardle, 1970b; Burrows, 1977).

Interpretation of the observed features indicative of instability in the vegetation presents a number of difficulties for the investigator. It must firstly be established that there exists a state of disequilibrium, as opposed to a steady-state equilibrium. Some evidence of past or future changes may be more apparent than real. Thus, for example, tree seedlings found beyond the margin of the community to which their parent trees belong will not become established and grow to maturity if the site is unfavourable to their development. The lack of small-sized trees in a population containing mature trees cannot be directly interpreted

Figure 1. Present distribution of Nothofagus forest in the North Island.

After Wardle (1967); Wardle (1970a); N.Z. Forest Service Mapping Series No. 6, Sheets 3, 4, 5, 6, 7, 10, 13, 14 (1970 to 1979); N.Z. Forest Service Mapping Series No. 15 (1974).

Small outliers close to, and enclaves lacking Nothofagus within the main areas of distribution are not shown.

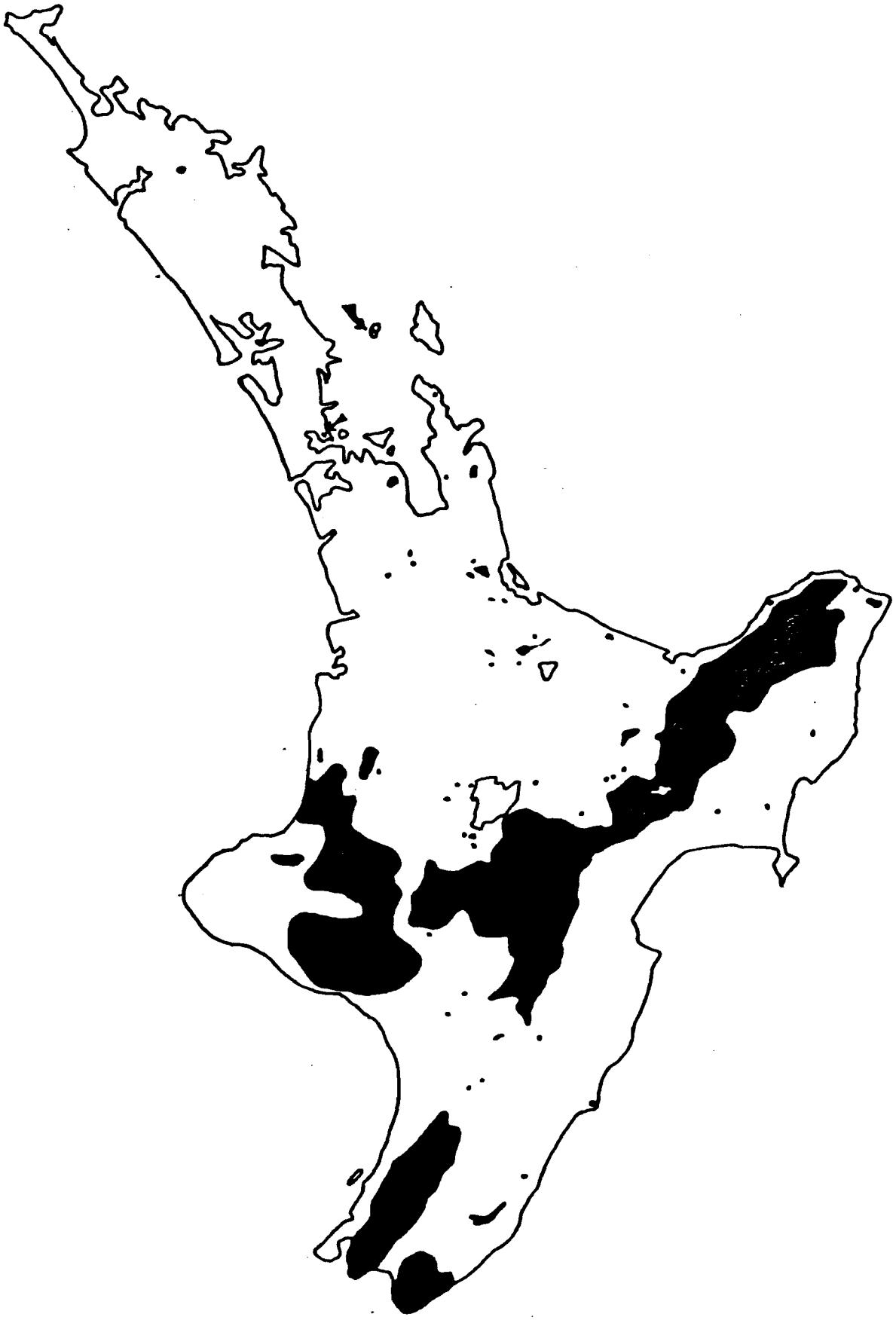

Figure 2. Present distribution of Nothofagus forest in the South Island. After Wardle and Mark (1956); Wardle (1967); Wardle (1970a); N.Z. Forest Service Mapping Series No. 15 (1974).
Small outliers close to, and enclaves lacking Nothofagus within the main areas of distribution are not shown.

as an age-gap in the population structure, because of the sometimes highly variable relationship between stem size and age in long-lived tree species, because of possible age-specific changes in growth rates, or because of the particular mode of regeneration of the species concerned. Direct observation of vegetation change is not always possible because of the long time periods involved; change may take place, for instance, over periods of hundreds or thousands of years. The nature and intensity of past changes, and the likely future states of the vegetation, must therefore be indirectly inferred. It is not always apparent whether the inferred instability is of local or widespread occurrence. The universality of the phenomena must be established.

In order to determine the causal factor or factors responsible for the observed phenomena, it is useful to distinguish the various types of vegetation change, both autogenic and allogenic (see Watt, 1947; Odum, 1971; Oliver & Stephens, 1977; White, 1979). Some changes can be related to endogenous cycles of senescence and replacement within a community; some are consequent on natural disturbances which give rise to primary and secondary successions; and some are caused by gradual, long-term changes in the physical and biotic environment.

A variety of explanations for the inferred instabilities in the New Zealand vegetation have been advanced. These include the effects of the Pleistocene glaciations (Cockayne, 1928; Willett, 1950; Wardle, 1963a) a resolution of the long-standing competitive interaction between gymnosperm and angiosperm groups (Cockayne, 1928; Robins, 1962), recent climatic fluctuations (Raeside, 1948; Holloway, 1954; Wardle, 1963b; McKelvey, 1963; etc), the effects of human activities (Cumberland, 1962; Molloy *et al.* 1963) and faunal changes associated with the arrival of man in New Zealand (Fleming, 1977; Wardle, 1979).

The description of a wide range of phenomena in South Island forests by Holloway (1954) and the postulation of climatic causes has had a particular importance in New Zealand forest ecology. Holloway attributed many apparent instabilities in the forests to a single cause; a deterioration in regional climates involving a decrease in temperature and rainfall beginning at about 1200 A.D.

While Holloway's hypothesis of climatic deterioration has stimulated a great deal of ecological research in New Zealand forests, its applicability and universality remain unclear. Evidence in support of the hypothesis has been provided by many authors

(for example, Nicholls, 1956; McKelvey, 1963, 1973; Wardle, 1963b, 1977, 1979), but other evidence and argument suggest alternative explanations for the observed phenomena (Cumberland, 1962; Molloy, 1969; Clayton-Greene, 1977; Stewart & Veblen, 1981). The status of the hypothesis remains contentious. This is partly because the observed phenomena such as the 'regeneration gap' have not been adequately described in quantitative terms, and partly because of the paucity of reliable information on past climates and biota and the regeneration modes of the species.

In this study, two of the apparent instabilities commonly found in New Zealand vegetation, namely the regeneration gap of podocarp species and the continuing expansion of range in *Nothofagus* are examined in a part of North Westland where they are both evident. An attempt is made to provide a better factual basis for testing Holloway's hypothesis and for answering the following questions: (i) do the apparent instabilities in the vegetation represent steady-state or non steady-state conditions? (ii) how widespread are the phenomena? (iii) are the phenomena related to a single causal factor or event? (iv) what is that factor or event or set of factors? (v) what changes in the vegetation can be predicted for the future?

The two phenomena which are the subject of this thesis will now be introduced more fully in turn. The specific aims of the thesis will also be described.

Geographical distribution and migration of *Nothofagus*

The distribution of *Nothofagus* in New Zealand shows a broad correlation with climatic and site conditions; in general *Nothofagus* is found in the cooler and wetter areas or elsewhere where site conditions are sub-optimal for tree growth and where competition from other species is lessened (Cockayne, 1926; Wardle, 1970a). However, there are many areas outside the existing range which appear to be suitable for one or more of the four species. In the North Island *Nothofagus* is unexpectedly absent from Mount Egmont, the southern Ruahine Range, the northern Tararua Range and most of the Hauhungaroa Range. Beech forest is absent from Stewart Island and from large areas of central Canterbury, and western Southland. The largest discontinuity in distribution is the 165km long section of central Westland which is occupied by podocarp-

hardwood forest in contrast to the extensive beech forests of north and south Westland. The study area is located at the northern end of this discontinuity.

Although the boundaries of *Nothofagus* appear to be static in some parts of New Zealand, there is evidence from many places of a recent expansion in the range of one or more of the species. Static boundaries have been described for Peel Forest in south Canterbury (Allan, 1926), in the southern Tararua Range (Franklin, 1967) and in the Ruahine Range (Elder, 1965). Evidence of an expanding range comes from Southland and Westland (Holloway, 1954), the Paringa district in south Westland (Wardle, 1980a), the northern Tararua Range (Wardle, 1962; Franklin, 1967), the Urewera forests (McKelvey, 1973) and the Kaimanawa Ranges (Elder, 1962). Further examples of *Nothofagus* expansion in areas disturbed by human activity have also been described (McQueen, 1951; Elder, 1941; Calder & Wardle, 1969; Wardle, 1970b; Burrows, 1977).

The *Nothofagus* boundaries in north Westland have only been described in general terms (Holloway, 1954; Franklin & Nicholls, 1974); accurate maps of the distribution of the four species are not available and there has been only a limited description of the migratory patterns in this area (Holloway, 1954).

Nothofagus spreads through the dispersal of seeds, either by marginal expansion from existing stands or by the establishment of new colonies at a distance from parent stands (McQueen, 1951; Holloway, 1954; Preest, 1963; Wardle, 1980 a,b). Long-distance dispersal of seed is considered to be by water carriage along rivers and streams, or by wind dispersal. Long-distance dispersal by wind appears to be an infrequent event with a limited range in the order of 4-6km. (Burrows, 1977; Wardle, 1979).

Migration rates for *Nothofagus* in New Zealand have been estimated by Franklin (1967) and Wardle (1980a). Franklin did not provide quantitative evidence for his estimate or describe the method of estimation. Wardle's estimate of migration rate applies to marginal spread from existing stands.

Holloway (1954) considered the migration of *Nothofagus* evident in South Island forests to be a relatively recent event beginning about 800 years ago. Palynological and other fossil records from a wide range of South Island locations (e.g. Moar, 1971; Wardle & McKellar, 1978) have shown, however, that the expansion of *Nothofagus* has proceeded throughout most of the postglacial and need not necessarily be related only to climatic change within the last 1000 years.

A better understanding of migration rates and the relative contributions of marginal spread and long-distance dispersal to the overall expansion of range would be valuable in interpreting the present and past distribution patterns of *Nothofagus*. *Nothofagus* has a major significance in Southern Hemisphere biogeography (Cranwell, 1963; Darlington, 1965) and a good understanding of this migratory behaviour is essential to the interpretation of its present and past distribution throughout the Hemisphere.

The absence of *Nothofagus* from central Westland has been attributed to the greater intensity of the Pleistocene glaciations in this region compared with peripheral areas, together with the subsequent slow expansion of *Nothofagus* from refugia to the north and south during the postglacial period (Cockayne, 1928; Willett, 1950; Wardle, 1963a). While this historical explanation is widely accepted, there have been differences of opinion about the course of forest development during the late Quaternary and in particular the extent of the surviving forest in the South Island during glacial periods and the subsequent rates of expansion from the refugia. . Willett (1950) considered that the disruptive effects of the ice sheets and the adverse periglacial climate would have caused the retreat of forest to limited coastal areas in the north and north-east of the Island. However, evidence from the present distributions of endemic species and *Nothofagus* forest (Wardle, 1963a; Burrows, 1965) and the postglacial fossil record (Moar, 1973; Lintott & Burrows, 1973; Wardle & McKellar, 1978, Dodson, 1978) suggests a much wider distribution of forest refugia.

A recent study (Wardle 1980a) examined *Nothofagus* migration rates and fossil record in the Paringa district of south Westland. Wardle suggested a likely location for glacial period refugia in that district, and the likely directions and extent of postglacial spread. This is the only detailed study of glacial and postglacial distributions of *Nothofagus* to date.

The inadequacies in our present knowledge of *Nothofagus* distributions and migration described above have led to the following specific aims for this investigation:

(i) to describe the present geographical distributions of the four *Nothofagus* species in north Westland;

(ii) to determine the present stability of the beech forest boundaries (whether expanding, stationary or retreating), and examine the effects of climatic, site and topographic factors on the position of the boundary;

(iii) to compare the effectiveness of the different modes of dispersal, including long-distance dispersal of seed, and to estimate rates of migration on different sites;

(iv) to determine the status of the beech forest outliers (whether invasion nuclei or relict stands);

(v) to reconstruct the postglacial distribution of *Nothofagus* in the study area using estimated migration rates, inferred migration routes and other knowledge of late Quaternary landforms and climates.

Regeneration failure in forest tree species

The term 'generation gap' applied to forest tree populations refers to the absence, rarity or infrequency of individuals in the younger age classes. The nature and possible causes of this widespread phenomenon, which is common among New Zealand gymnosperm species, have been reviewed by Molloy (1969), Wardle (1973a, 1979) and Burrows & Greenland (1979).

It is useful in interpreting population structures to define more rigorously the significance of the 'generation gap'.

In populations exhibiting a 'regeneration gap', seedlings, saplings, poles and younger canopy trees are under-represented compared with their expected frequencies for stable, continuously regenerating populations (Meyer, 1952; Hett & Loucks, 1976). The size or age frequency distribution for a stable population is represented by an inverse, J-shaped curve and can be described by the function $y = y_o\, x^{-b}$, where y is the frequency in any size or age class, y_o the initial input into the population, x the size or age value, and b the mortality rate (see Fig 3).

The interpretation of past regeneration rates from population size structures has several limitations. The correlation between the size of an individual and its age may be weak, particularly for mature canopy trees (e.g.Herbert, 1980). The population age structure reflects both regeneration and mortality rates in the past, and information on both these parameters is needed before a satisfactory deduction of population history can be made (see Harper, 1977). Generally, the assumption is made that age-specific mortality rates have not changed significantly in the past and the population structure is interpreted as representing fluctuations in the past rate of regeneration.

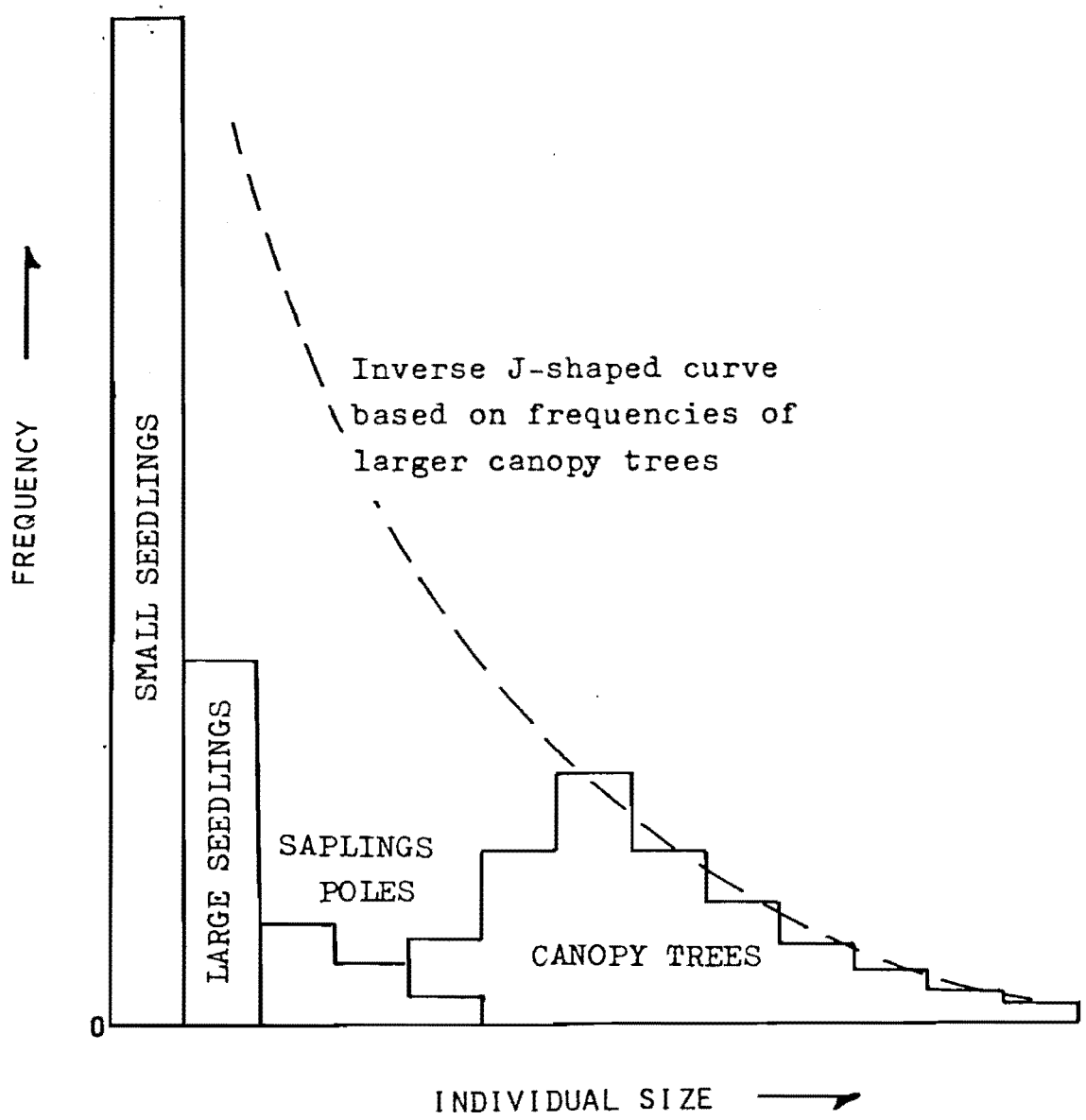

Figure 3. The general form of the size structure in New Zealand gymnosperm populations. (After Wardle, 1963b, 1978; Clayton-Greene, 1977; Herbert, 1978; this study, Figure 29 and Table 14.)

Thus, in podocarp populations the observed 'regeneration gap' is considered to represent a lower rate of regeneration in the recent past than during the period when the existing canopy trees became established. (e.g. Wardle, 1963b)

The 'regeneration gap' has been described in most native gymnosperm species and on a wide range of sites throughout New Zealand (Table 1).

Holloway (1954) dated the beginning of the period of failed gymnosperm regeneration at 1200 A.D. Other workers, using better estimates of tree ages, have dated the beginning of the period at:

1650 A.D.	(Nicholls, 1956)
1600 A.D.	(McKelvey, 1953)
1600 A.D.	and as early as 1300 A.D. in some stands (Wardle, 1963b, 1978)
1500 A.D.	(Grant, 1963)
1600 A.D.	(Barton, 1972)

In some areas a steady decline in the regeneration rate appears to have preceded by about 100 years the time at which regeneration failed completely (Wardle, 1963b).

An upsurge in the rate of regeneration beginning in c. 1850 A.D. has been inferred from rimu *(Dacrydium cupressinum)* population size structures in the South Island (Wardle, 1963b). This interpretation relies on unquantified assumptions about the future survivorship of rimu seedlings and saplings. An abundance of podocarp saplings and poles has also been observed in some podocarp-dominant forests on the Volcanic Plateau where the 'regeneration gap' is evident (Beveridge, 1973; Herbert 1978), but not in other forests of similar composition (McKelvey, 1973). Evidence for regeneration in the past 100 years is confused by the effects of introduced browsing animals. In some instances, for example Whirinaki forest, browsing by deer and opossums has eliminated large podocarp seedlings or retarded their growth (Beveridge, 1973).

Although the 'regeneration gap' is a common feature of gymnosperm populations there are exceptions where no decline in regeneration is apparent. These include kahikatea *(Podocarpus dacrydioides)* on swampy sites and young alluvium (Cockayne, 1928; Wardle, 1974) and cedar *(Libocedrus bidwillii)* on montane sites in the Waikato district (Clayton-Greene, 1977). Regeneration of rimu on outwash terraces in Southland and Westland (Holloway, 1954; Franklin, 1968; Wardle, 1978), in some sites near the upper altitudinal limits of

Table 1. Observations of a 'regeneration gap' in New Zealand gymnosperm populations.

Species	Site and location	References
Dacrydium cupressinum	Hill slopes (throughout), alluvial and glacial outwash terraces (Westland), pumice basins (Volcanic Plateau)	Holloway (1954), Nicholls (1956), Druce and Atkinson (1959), Cameron (1954), Grant (1963), Wardle (1963b, 1963c, 1978), McKelvey (1963, 1973), Burrows *et al.* (1975)
D. biforme	High altitude hill slopes (Ruahine Range)	Elder (1965)
Podocarpus dacrydioides	Hill slopes (Westland, Taranaki, West Taupo, Urewera, Southland), pumice basins (volcanic plateau)	Holloway (1954), Nicholls (1956), Grant (1963), McKelvey (1963, 1973)
P. totara	"	"
P. spicatus	Hill slopes, colluvial slopes, alluvial terraces (throughout), pumice basins (volcanic plateau)	" Wardle (1963b, 1978)
P. ferrugineus	Hill slopes (West Taupo)	McKelvey (1963)
Libocedrus bidwillii	High altitude hill slopes and moraines (Dunedin, Westland, Ruahine Range)	Wardle (1963b, 1978), Wardle and Mark (1956), Elder (1965)
Agathis australis	Hill slopes, rolling country (Northland, Hunua Range, Coromandel)	Barton (1972) Beveridge (1977)

the species and on lowland sites on Stewart Island (Wardle, 1963b), appears to have been more abundant than elsewhere. The more abundant regeneration of rimu in some locations has been related to low soil fertility favouring the gymnosperms at the expense of competing species and to cooler and moister climatic conditions.

In contrast to the situation in undisturbed forests, prolific gymnosperm regeneration often occurs on freshly-exposed soil surfaces and in early successional shrubland and forest communities (Franklin, 1968; Molloy, 1969).

Other New Zealand tree species apart from gymnosperms show partial or complete regeneration failures within the life span of existing trees. The major examples noted are *Nothofagus menziesii* and *N. fusca* (Grant, 1963; Burrows & Greenland, 1979) and *Metrosideros umbellata* (Wardle, 1971b). It is not known if the population age structures of these species are similar to those described for gymnosperm populations.

Many workers have published observations of the 'regeneration gap' in New Zealand gymnosperms (see Table 1). Despite this, satisfactory data for a full quantitative analysis of the phenomenon are not available as a basis for a theoretical explanation. Population age structures are available for only two species: *Libocedrus bidwillii* in the Waikato district (Clayton-Greene, 1977) and *Dacrydium cupressinum* on the Volcanic Plateau (Herbert, 1980; Katz, 1980). Some size structures have been described (e.g. Wardle, 1963b, 1963c, 1-78) but these are difficult to interpret because of the variable or unknown relationship between size and age in these long-lived species.

The deduction of past regeneration rates from population size and age data requires some knowledge of regeneration patterns, including the requirements for seedling establishment and growth, and of mortality rates at each stage of development. As an example, the abundance of seedlings and saplings in some stands could represent a recent upsurge in the rate of regeneration or, alternatively, future recruitment to the canopy could be negligible following the normal high mortality amongst younger individuals. The impact of introduced animal predators must also be evaluated and in some cases human interference must be considered.

The approach taken in this study of the 'regeneration gap' was to compare the population structures and regeneration requirements of the seven major canopy tree species of the lowland forests in the study area. The species studied were rimu *(Dacrydium cupressinum)*

miro *(Podocarpus ferrugineus)*, southern rata *(Metrosideros umbellata)*, *Quintinia acutifolia*, kamahi *(Weinmannia racemosa)*, hard beech *(Nothofagus truncata)* and red beech *(N. fusca)*. In populations of some of these species a regeneration failure is evident; in others it is not. Particular emphasis was placed on rimu because of the pronounced 'regeneration gap' in this species and because it has been the subject of a number of investigations throughout the country.

The specific aims were to describe the following features of populations of the seven canopy tree species:

(i) complete size structures;

(ii) an age structure in the case of rimu;

(iii) the relationships between stem size or seedling height and age (in order that size structures from a wide range of localities can be interpreted in age terms);

(iv) the growth and survival rates of seedlings;

(v) the course of recruitment from the seedling stage to attainment of the upper canopy level and the factors influencing this development.

The role of natural catastrophe in regeneration, and the effects of introduced browsing animals were also considered.

Information from this study is used to evaluate the spatial and temporal characteristics of the 'regeneration gap' and its possible causes. The regeneration modes of the species studied are characterised and compared with regeneration patterns in tropical and north temperate forests.

CHAPTER TWO

THE STUDY AREA AND STUDY STANDS

The study area comprises the southern portion of the Paparoa Range and the adjoining Grey-Inangahua Depression, and is bounded by the Alpine Fault in the east and the coastline to the west. The boundaries of the study area, which covers some 2400 km^2, are shown in Figure 6 (section 4.1)

Selection of the study area boundaries

The boundaries of the study area were chosen to include the broad transition zone between the beech-podocarp and podocarp-hardwood forest types in north Westland. That part of the transition zone to the east of the Alpine Fault was excluded, however, as *Nothofagus* boundaries in this area are under investigation by Dr C.J. Burrows of the University of Canterbury. The western boundary of the study area was provided by the coastline and the eastern boundary by the Alpine Fault which separates the Grey-Inangahua Depression from the Southern Alps.

The study area provided a wide range of locations for detailed study of population structure and dynamics, because of the diversity of growing sites and local climates in the area and the availability of large areas of indigenous forest ranging in altitude from near sea level to timberline.

Geology and physiography

The southern Paparoa Range occupies the north-western corner of the study area. This part of the Paparoa Range is geologically diverse, being composed of pre-Cambrian greywacke of the Greenland Group, Coal Measures of the Paparoa Group and siltstones of the Arnold Series (Bowen, 1964). Slopes are generally less steep and more stable compared with the area of the Southern Alps which adjoins the study area.

The Grey-Inangahua Depression is a geosyncline bordered by the Paparoa Range to the west and a series of mountain blocks to the east (Bowen, 1964; Gregg, 1964; Warren, 1967). The Depression was formed during the late Cenozoic era.

Upper Tertiary (siltstone, limestone and mudstone) and Lower Pleistocene (glacial outwash gravel) sediments provide the rocks in most of the western portion of the Depression, and Upper

Pleistocene sediments (glacial outwash and till) predominate in the eastern portion. The Upper Pleistocene deposits represent three glaciations - the Waimaungan, Waimean and Otiran (Bowen, 1964; Suggate, 1965).

Isolated blocks of granite of the Tuhua Group protrude within the southern portion of the study area. These blocks include Lake Hill Ridge and Granite Ridge to the south of Lake Hochstetter and the more massive Hohonu Range in the south.

Much of the central portion of the study area comprises blocks of deeply dissected gravel or siltstone forming hill country separated by broad river valleys entrenched in flights of post-glacial and Otiran terraces. Most hill slopes fall within the 25^0-35^0 range and slopes commonly terminate in steep banks which border deeply-engorged streams. Small remnants of the original, much-eroded high-level terraces are found amongst the hill country. Rolling moraines and outwash cover large areas between the blocks of hill country and the edge of the mountain ranges to the east. The sequence of Upper Pleistocene deposits which form the moraines have been described and mapped by Suggate (1965). Table 2 shows the sequence of deposits and their correlation with glacial periods.

Table 2: Upper Pleistocene deposits found in the study area.

Formation	Glacial Advance	Stage
Moana	Kumara - 3	Otira Glacial
Loopline	Kumara - 2_2 & Kumara - 2_1	Otira Glacial
Waimea	Kumara - 1	Waimea Glacial
Cockeye	Hohonu	Waimaunga Glacial

Lower Pleistocene deposits - Old Man Gravels of the Wanganui Series - are also found in the northern part of the study area (Bowen, 1964)

A narrow strip of sand dunes is found along the coast, together with limited areas of old marine benches composed of sands and gravels.

Geological maps at a scale of 1 : 250 000 are available for the area (Bowen, 1964; Gregg, 1964; Warren, 1967).

Soils

The soils of the area and their distribution have been described in general surveys (Gibbs *et al.*, 1950; N.Z. Soil Bureau, 1968, 1969). A more detailed survey with 1 : 50 000 soil maps covering most of the study area (Adams & Mew, 1976) has been partially published (Mew, 1980). In this latter survey the soil sets originally mapped (N.Z. Soil Bureau, 1968, 1969) have been subdivided into a greater number of soil mapping units.

Seven main soil groups can be recognised (Mew & Leamy, 1977). Recent soils occur on the flood plains; yellow-brown earths and gley soils occupy most of the hill country and some terraces; gley podzols and, in limited areas, podzols occupy the intermediate and high terraces. Yellow-brown sands are found on the coastal sand dunes and organic soils on swampy depressions on floodplains and outwash terraces.

Soils associated with beech-podocarp and podocarp-hardwood forest types show differences in the type of organic matter and its down-profile movement. (Mew & Leamy, 1977). Other variations in soil characteristics within the main soil groups of the area can be related to rainfall gradients and differences in micro-topography and parent material.

Climate

The climate of the Westland region is classified as cool and superhumid (Garnier, 1958). Summers are cool and winters mild. The mean daily air temperature at Totara Flat in the centre of the Grey-Inangahua Depression is 16.2^{0}C in January and 5.6^{0}C in July, and 70-80 ground frosts are recorded per annum (N.Z. Meteor--ological Service, 1977). Precipitation (largely as rainfall) is high to very high and is well distributed throughout the year. Rainfall minima occur during early summer (December and January) and winter (June, July and August). Annual rainfall varies from 2000 mm near Totara Flat to greater than an estimated 5600 mm in the high altitude areas of the Paparua and Hohonu Ranges (Figure 14). The centre of the Grey-Inangahua Depression is partially in a rain shadow from the Paparoa Range.

The predominant wind direction is from the north-east at Totara Flat and from the east, south-east and west at Hokitika (N.Z.Meteorological Service, 1977).

Vegetation

Temperate, evergreen forest is the predominant natural vegetation, although limited areas of swampland, subalpine scrubland, seral scrubland and subalpine tussock grassland are also present.

The forest vegetation of the study area has been described in broad terms by Holloway (1954), Wardle (1970a) and Franklin & Nicholls (1974). Franklin & Nicholls provide a map showing the present distributions of eight forest classes. A series of unpublished N.Z. Forest Service volumetric survey maps on a scale of 1 : 15840 (Masters *et al.* 1957) describe the distributions of forest types which are delineated on the basis of dominant tree species and topographical features.

Three major forest classes can be recognised as the basis of the presence or absence of the different groups of canopy tree species: Beech, Beech-podocarp-hardwood (commonly, Beech-podocarp) and Podocarp-hardwood. This technology is commonly used in forestry (d. Kirkland & Trotman, 1974. It should be noted that in this usage the term hardwood does not include *Nothofagus* species.

All four species of *Nothofagus (N. fusca, N. truncata, N. solandri* var. *cliffortioides*, and *N. menziesii)* occur as canopy trees. In upland forests the *Nothofagus* spp. form nearly pure stands with occasional *Metrosideros umbellata, Weinmannia racemosa, Phyllocladus alpinus, Libocedrus bidwilli* and *Dacrydium intermedium* ('Beech' forest type). In lowland forests of the 'Beech-podocarp' type, the *Nothofagus* species are the predominant canopy trees in association with *Dacrydium cupressinum, Quintinia acutifolia, Weinmannia racemosa, Metrosideros umbellata* and *Podocarpus ferrugineus* on hill slopes, *Podocarpus spicatus* and *P. dacrydioides* on alluvial floodplains, and *Phyllocladus alpinus, Librocedrus bidwilli, Dacrydium colensoi, D. biforme, Podocarpus hallii* and *Elaecarpus hookerianus* on glacial outwash terraces. In 'Podocarp-hardwood' forest types the *Nothofagus* species are absent and the other species described above form the canopy.

Most of the stands selected for detailed study were located in lowland hill country sites. A detailed description of the species' composition and canopy structure of these stands is now given. (Further details of the study stands are shown in Table 4.)

The upper canopy layers are composed of the emergent crowns of *Dacrydium cupressinum* with a dense foliage matrix of predominantly *Quintinia acutifolia* and *Weinmannia racemosa* in podocarp-hardwood forest and *Nothofagus fusca* and *N. truncata* in beech-podocarp forest. Scattered *Metrosideros umbellata, Podocarpus ferrugineus, Elaeocarpus dentatus, E. hookerianus* and *Phyllocladus alpinus* are also present in the canopy. *Nothofagus truncata* occupies ridge crests and upper slopes while *N. fusca* is largely confined to gullies and lower slopes. *Podocarpus hallii* was a minor component of the canopy until recently. Nearly all the trees of this species have died within the past 10 years and surviving trees appear unhealthy. Emergent *Dacrydium cupressinum* trees or small groups of trees form an open overstorey. Both *D. cupressinum* and *M. umbellata* are more frequent on ridge crests than on other sites.

Maximum tree heights in the canopy are as follows:

Dacrydium cupressinum	25-34 m
Nothofagus fusca, N. truncata	22-30 m
Metrosideros umbellata	20-26 m
Quintinia acutifolia, Weinmannia racemosa, Podocarpus ferrugineus and *Phyllocladus alpinus*	14-18 m

The understorey is relatively open where the overhead canopy is continuous, but dense thickets of shrubs develop within canopy gaps. The understorey is largely comprised of juveniles of the canopy species, particularly those of *Q. acutifolia, W. racemosa* and the *Nothofagus* species. Other important subcanopy species are *Coprosma foetidissima, Myrsine salicina, Griselinia littoralis, Neomyrtus pedunculata* and *Cyathodes fasciculata* (on ridge crests). Minor species in the understorey include *Myrsine australis, M. divaricata, Coprosma australis, C. lucida, Pseudowintera colorata, Ascarina lucida* (within 25 km of the coast), *Metrosideros parkinsonii, Pseudopanax crassifolium, P. simplex, P. colensoi* and the lianes *Ripogonum scandens, Metrosideros diffusa, M. fulgens, M. perforata, Rubus cissoides* and *Parsonsia heterophylla*. *Aristotelia serrata, Fuchsia excorticata, Schefflera digitata, Carpodetus serratus* and *Melicytus ramiflorus* are commonly found in gullies and newly formed large canopy gaps. The tree ferns *Cyathea smithii* and *Dicksonia squarrosa* occasionally form dense colonies in gullies or on lower slopes and are infrequent or absent elsewhere.

Table 3: Preferred sites of the *Nothofagus* species in north Westland

Site[1]	*Nothofagus* species			
	N. fusca	*N. truncata*	*N. solandri* var. *cliffortioides*	*N. menziesii*
Flood plain	+	-	-	+
Hill country - ridges	-	+	-	-
Hill country - lower slopes and gullies	+	-	-	-
Glacial outwash terraces and rolling morainic deposits - better drained sites	-	+	-	-
Glacial outwash terraces and rolling morainic deposits - poorly drained sites	-	-	+	-
Steepland and mountain ranges - mid slopes	+	-	-	+
Steepland and mountain ranges - upper slopes	-	-	+	+

[1] Physiographic classification follows Mew *et al.* (1975).

The ground layer is generally open, with the ground surface covered by litter or moss colonies. Apart from the seedlings and suckering shoots of subcanopy and canopy species, extensive colonies or small clumps of ferns may be present. *Blechnum discolor* is the major fern species in the groundlayer. *Gleichenia cunninghamii* forms large colonies on ridge crests and upper slopes. Other ferns include *Blechnum capense, B. fluviatile, B. minus, Asplenium bulbiferum, A. lucidum, Polystichum vestitum, Rumohra hispida, Todea superba, Lindsaea trichomanoides, Trichomanes strictum, T. reniforme, Hymenophyllum villosum, H. multifidum* and *Grammitis billardieri*. Other species in the ground layer include *Tmesipteris tannensis, Nertera dichond raefolia, Libertia pulchella, Dianella nigra, Uncinia* spp., *Microlaena avenacea* and *Freycinetia banksii* (which forms extensive colonies within 20 km of the coast).

The four *Nothofagus* species in varying combinations are able to occupy most forest sites within north Westland, with each species showing a preference for a particular range of sites (Table 3). Each species also occupies a broader range of sites as a minor stand component. For example, *N. menziesii* is normally present as a minor canopy or subcanopy tree in association with *N. solandri* var. *cliffortioides* or *N. truncata* on poorly-drained terraces.

The site preferences of *Nothofagus* may be related to the different nutrient requirements of the species (Adams, 1977). (For preferred sites of *Nothofagus* in north Westland see Table 3 opp.)

Human interference

Most of the study area has been modified by human activity associated with goldmining, timber exploitation, farming and the establishment of forestry plantations. The forests on the flood plains have been largely cleared for farming, and limited areas of the lowland hill country forests have been cleared for the establishment of exotic conifer plantations. Of the remaining lowland forest, logging has modified all but minor areas. A reserve system involving Scenic Reserves and Ecological Reserves (in State Forest) is currently being established.

The effects of goldmining on the vegetation are largely confined to stream and river beds and flood plains. Goldminimg involved dredging and sluicing of most stream and river beds, removal of timber from forests in the immediate vicinity of mining activity, the construction of water races and the clearing or firing

of forest in small areas close to habitation or along tracks.

The impact of human activity on the forests can be seen from the topographical maps covering the study area (Figs 8,9, 10,11,12). The extent of human modification has important implications for this study. It was not possible to find suitable stands for detailed population studies on flood plains. Some outliers of beech forest and sections of the beech forest boundaries have been destroyed. Many of the remaining boundaries have been modified by logging or farming activities and were not suitable for detailed migration studies.

Introduced animals

Red deer *(Cervus elaphus)*, brush-tailed possums *(Trichosurus vulpecula)*, stoats *(Mustela erminea)*, black rats *(Rattus rattus)*, and mice *(Mus musculus)*, are widespread. Goats *(Capra hircus)* and pigs *(Sus scrofa)* have a localised distribution.

The most important understorey browsing animal, the red deer, arrived in the study area c. 1920 and reached peak densities in the 1930's (Clarke, 1976). Present red deer densities are low.

Postglacial forest history

The postglacial forest record within the study area indicates the continuous presence of a rimu dominant, podocarp-hardwood forest similar in composition to present day forests since about 9 000 years B.P. (Moar, 1971; Pocknall, 1980). The entry of *Nothofagus* at c 2 400 years B.P. is also recorded. Slope stability characteristics in the Notown area have been interpreted as indicating a stable vegetation cover, assumed to be forest, throughout the postglacial (O'Loughlin & Gage, 1975). Postglacial forest history of the study area is discussed further in section 5.5.

The study stands

Ten stands within the study area were chosen for quantitative study. The stands were placed to include a wide range of lowland forest sites in accessable locations, particularly on hill country. In addition, one upland forest site was selected for a quantitative study of the beech boundary. Their locations are shown in Figure 4, and details of each stand are given in Table 4. In selecting stands for study, care was taken to avoid areas disturbed by human activity. Within each stand, a variable area of from 5 to 10 hectares was sampled for different purposes. This meant that a wide range of aspects (depending on the local relief patterns) and

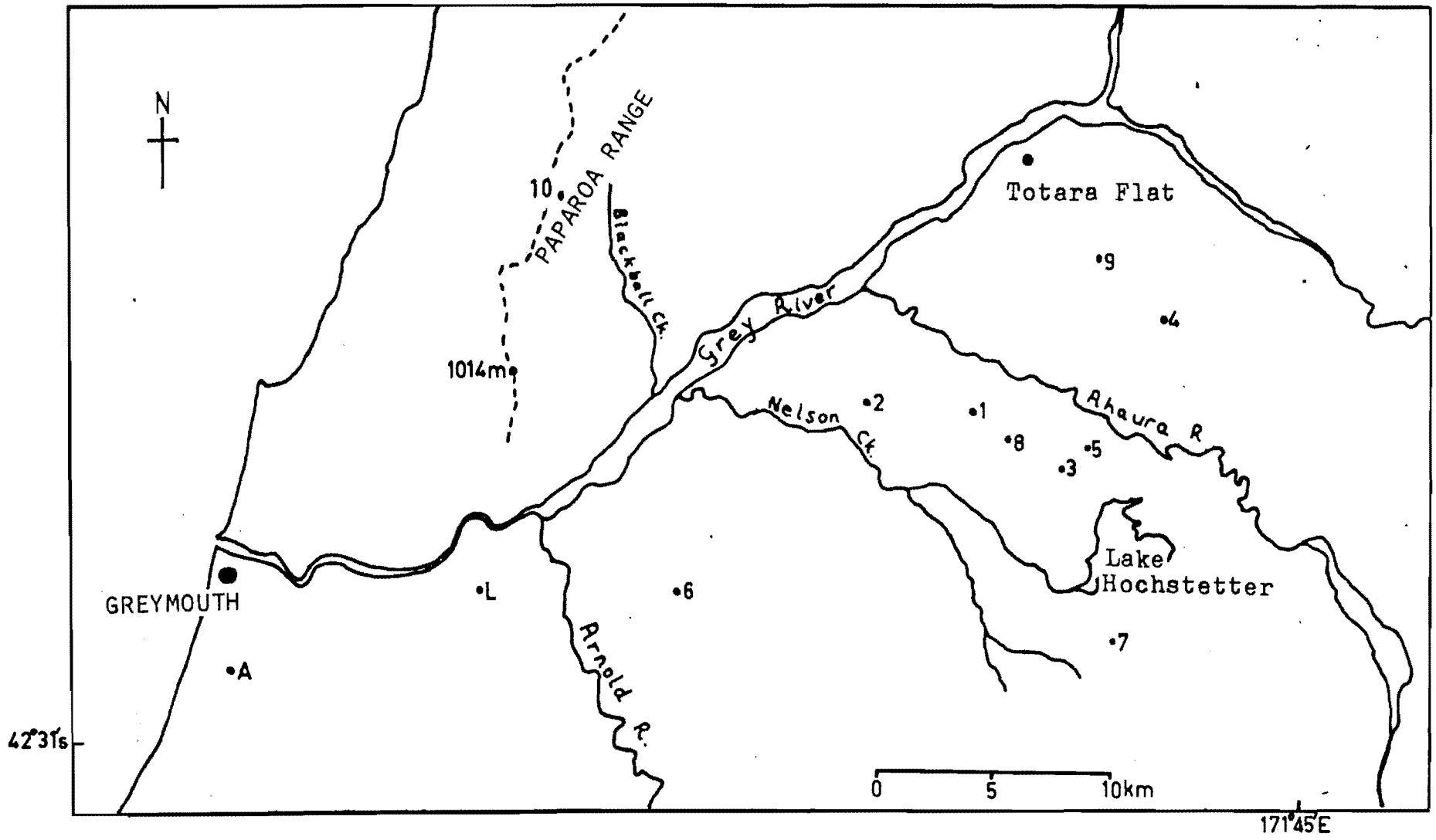

Figure 4: Location of study stands

Table 4. Descriptions of the study stands:

Stand No.	Location	Forest Type	Soil parent material[1]	Altitude (m a.s.l.)	Annual rainfall (mm)[2]	Approximate map reference (NZMS 1 series)
1	Callaghans Ridge	Podocarp-hardwood	Glacial outwash gravels (Nukumaruan and Cockeye)	300-350	2800-3200	S45/102989
2	Prices Creek	Podocarp-hardwood	Glacial outwash gravels (Nukumaruan and Cockeye)	150-260	2800-3000	S45/023952
3	Kellys Creek	Beech (*Nothofagus truncata* - *N.fusca*) - podocarp and Podocarp-hardwood (terrace and slope)	Glacial outwash gravels (Cockeye)	300-400	3200-4000	S45/114923
4	Napoleon Hill	Beech (*N.truncata* and *N.fusca*) - podocarp and podocarp-hardwood	Glacial outwash gravels (Nukumaruan)	240-300	2800-3200	S45/163989
5	Irishmans Creek	Beech (*N. fusca*) - podocarp and podocarp-hardwood	Glacial outwash gravel (Nukumaruan)	300-370	3200-4000	S45/128932
6	Notown	Podocarp-hardwood	Siltstone and sandstone (Waitotaran)	240-320	2800-3200	S44/940867
7	Lake Ridge	Podocarp-hardwood	Siltstone and sandstone (Waitotaran)	400-520	3200-4000	S45/134844

Table 4. Descriptions of the study stands.

Stand No.	Location	Forest Type	Soil parent material[1]	Altitude (m a.s.l.)	Annual rainfall (mm)[2]	Approximate map reference (NZMS 1 series)
8	Upper Callaghans Creek	Podocarp-hardwood (terrace)	Glacial outwash gravels (Cockeye)	370	3200-4000	S45/121927
9	Half Ounce Creek	Beech (*N. truncata*) - podocarp	Glacial outwash gravels (Old Man)	210-270	1600-2000	S45/144018
10	Clarke Creek	Beech (*N. menziesii*)	Greywacke (Greenland)	920	4800-5600	S44/893050
Other stands mentioned in text:						
L	Lisbon Creek	Podocarp-hardwood	Calcareous siltstone	150-270	2800-3200	S44/845865
A	Aorangi Scenic Reserve	Podocarp-hardwood	Marine mudstone, siltstone and sandstone (Waiauan)	60-110	2400-2800	S44/730833

[1]After Bowen (1964)

All stands are on hill slopes unless otherwise indicated

[2]Estimated range from isohyetal map - Figure 22.

growing sites from ridge crests to lower slopes were available for population sampling. The steep-sided gullies with their distinctly different vegetation were not sampled.

Stands 1, 2, 3, 5 and 7 are located in Hochstetter State Forest, Stands 4 and 9 are in Granville State Forest and Stand 6 is in Mawhera State Forest. Stands 3, 5 and 8 are within the proposed Lake Hochstetter Ecological Reserve (to be administered by the N.Z. Forest Service) and Stand 10 is in the Roaring Meg Ecological Reserve, Paparoa State Forest.

The lowland forest stands cover an altitudinal range of 150 to 500 m a.s.l. This includes most of the altitudinal range of rimu in the study area which is from c 30 m a.s.l. to 610-660 m a.s.l.

Stand 3 (Kelly's Creek) was subdivided into terrace (Stands 3A and 3B) and hill slope (Stand 3C) sites. Stand 4 (Napoleon Hill) was subdivided into Stands 4A and 4B where hard beech and red beech respectively are dominant.

CHAPTER THREE

METHODS

3.1 FIELD SURVEY

An intensive field reconnaisance of the study area was undertaken on foot. Additional observations were made from roadways and from the air. Extensive surveys were carried out in the areas adjoining the study area, i.e. the Taramakau valley, the Punakaiki district and the Hokitika-Kumara district, and also in south Westland.

During field survey an attempt was made to walk through as much of the study area as possible, crossing topographical boundaries where possible and thereby sampling a cross section of the vegetation and landforms present in the area. Topographical maps (scale 1:63 360) and paired black & white aerial photographs (scale approx. 1:23 000) were used for navigation and interpretation of vegetation patterns. Geological maps on a scale of 1:250 000 (Bowen, 1964; Gregg, 1964; Warren, 1967) assisted in the interpretation of the landforms and soils encountered by providing information on soil parent materials and the relative ages of different surfaces.

The general aim of the field survey was to gain an understanding of forest patterns in the area, including the site preferences of individual species and the variation in community composition from site to site. Particular emphasis was placed on the distributions of the four *Nothofagus* species (see section 3.3), the nature of the beech forest boundary, the variation in the population structures of the main canopy tree species from place to place and the regeneration characteristics of the predominant species.

For each forest type[1] recognised on a line of travel the following observations were recorded:

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[1] forest type as defined by McKelvey & Nicholls (1957)

- topography
- slope
- aspect
- drainage
- canopy, shrub & ground species and their relative abundance
- nature of the ground cover
- presence of dead trees
- canopy condition (gaps, height)
- growth forms and diameters of canopy trees
- presence of browsing animals
- evidence of human interference

At the beech forest boundary, observations were made on the sizes of the beech trees forming the boundary and the dispersion of beech seedlings away from the boundary trees. Quantitative measurements at sections of the beech boundary are described in section 3.6. As an adjunct to more detailed work on population structures and regeneration in the stands selected for study (described in later sections), observations were made during field survey of the frequencies of the different life stages of canopy tree species and of the growing positions of seedlings, saplings and poles (in relation to microsite and overhead canopy conditions).

3.2 PERIOD OF STUDY

A total of 293 days were spent on field work from April 1974 to November 1978. Of this period, 177 days were spent on reconnaissance and 116 days on detailed population studies in the study stands.

3.3 MAPPING OF *NOTHOFAGUS* SPECIES DISTRIBUTIONS

The limits of distribution of the four *Nothofagus* species in the north Westland region were mapped using aerial photographs, ground investigation and existing records.

Existing information was available from several sources including two series of N.Z. Forest Service maps: (1) unpublished National Forest Survey forest type maps with a scale of 1:15 840 (Masters *et al.*, 1957) and (2) a forest class map with a scale of 1:250 000 (Franklin & Nicholls, 1974). These maps do not show the beech boundaries with any degree of accuracy, nor are the distributions of the individual species given. As well, the small beech forest outliers are generally not shown. The approximate distribution of *Nothofagus solandri* in north Westland is recorded by Wardle (1970a) and that of *N. menziesii* by Wardle (1967).

The mapping of the beech distributions was done largely from ground inspection, using vantage points where possible. Some reconnaissance was carried out from a light aircraft. From a distance, beech trees can be readily distinguished from other vegetation on the basis of foliage colour, crown texture and tree form. This is particularly so at the time of growth flush in November and December. The individual beech species can be recognised using these features although confirmation from leaf specimens was sometimes necessary, particularly to distinguish *N. fusca* and *N. truncata*. Hybrid individuals were identified from characters such as leaf size, shape, serration and venation, the presence of domatia (on leaves) and bark texture (on mature trees). Hybrid characteristics in the *Nothofagus* species have been described by Cockayne & Atkinson (1926), Cockayne (1926) and Poole (1951).

Vertical black & white aerial photographs were used as base maps. These photographs (scale 1:23 000 approx.) were taken between 1969 and 1973. The beech canopy was not reliably distinguishable on the photographs in some places. The beech boundaries were mapped on to the aerial photographs by a combination of field work and photo-interpretation and then transferred to 1:63 360 topographical maps (N.Z. Mapping Series 1, Department of Lands and Survey) from which other larger scale maps were derived.

Detailed boundary mapping was confined to the study area (see Fig 6). The remainder of the region beyond this primary area of study was mapped less precisely and with more emphasis on the published information. The locations of beech forest timberlines in the adjoining areas of north Canterbury were obtained from the N.Z. Forest Service mapping Series 6, scale 1:250 000, Sheet No. 19 (1974).

In some places the beech forest boundaries could not be mapped accurately because of the past removal of forest for exotic forestry and agriculture. The extent of forest clearance is shown on the topographical maps used in this study (Figs 8 to 12). Much of the remaining lowland forest has been modified by logging.

An attempt was made to record the location of the beech forest boundary using colour photographs taken during reconnaissance with a light aircraft and from vantage points on the ground. Photographs were taken from the aircraft at oblique angles from altitudes as low as 300m above the ground surface. Two types of

standard colour film ("Agfa 50S" and "Kodachrome II") were used but a satisfactory resolution of the different species' canopies could not be obtained.

During field reconnaissance, emphasis was placed on locating and visiting the outliers of the beech forest distribution. Where outliers were not visited an attempt was made to determine the *Nothofagus* species present by viewing the outliers through binoculars.

The areas of individual outliers were estimated using millimetre graph paper overlays on the outlier boundary marked on vertical aerial photographs in the case of outliers smaller than two hectares, and on 1:63 360 topographical maps in the case of larger outliers. Conversion factors obtained from aerial photographs took into account the flight elevation above the ground surface for each outlier.

The distances between the outliers and the potential parent stands were horizontal distances measured on 1:63 360 topographical maps between the geographical centre of the outlier and the margin of the potential parent stand. The potential parent stand is the nearest stand of beech forest which is larger than the outlier and which contains the same *Nothofagus* species as the outlier.

3.4 EXPERIMENTAL SOWING OF *NOTHOFAGUS* SEED

As a pilot experiment to investigate the role of mycorrhizae in *Nothofagus* seedling establishment away from beech forest, seed was oversown in podocarp-hardwood forest in the study area. Seed of the four *Nothofagus* species was collected from the ground at a number of locations in the Grey Valley in May, 1976 immediately following a heavy rainfall. Other litter was removed by sorting and by washing the nuts in tap water. A sample of the seed was dissected to check for viability. Seeds with developed embryos were assumed to be viable (see Bibby, 1953). The proportions of seeds with developed embryos were as follows:

N. truncata 66/155 = 43% *N. fusca* 26/116 = 22%

N. menziesii 17/97 = 18% *N. solandri* var. *cliffortioides* 16/133 = 12%

Within one day after collection the seed was sown on to three plots placed in undisturbed podocarp-hardwood forest at German Gully (Hochstetter State Forest) at least 300m distant from the nearest *Nothofagus* trees. Within each plot, seeds of each of

the four species were spread evenly over separate sub plots each 2m x 2m. Each plot was located beneath a canopy in places where there was little shrub or ground layer. In each plot the ground surface was largely covered with litter or moss colonies. Two of the plots were located on a high level, glacial outwash terrace and the third on an adjoining upper slope. The soils were gleyed with low to very low nutrient status (Adams & Mew, 1976). An estimated 200 to 600 viable seeds of each species were sown and a total of 299 seedlings germinated by November 1976. The seedlings, together with seedlings of similar age from nearby *Nothofagus* forest, were collected and assessed for vigour and degree of mycorrhizal infection in November 1978 when the seedlings had begun their third growing season. Mycorrhizae were examined microscopically on seedling roots stained in a 0.05% solution of trypan blue in lactophenol.

3.5 IDENTIFICATION OF MYCORRHIZAE IN ISOLATED *NOTHOFAGUS* STANDS

The roots of *N. fusca* and *N. solandri* var. *cliffortioides* trees growing in small stands isolated from the main *Nothofagus* range, were sampled and assessed for the presence of mycorrhizae using the method described above. Six stands in the Rotomanu district, north Westland, were sampled in December 1977. The stands were located from 3.5 to 10.0 km from the main beech forest boundary in the Grey Valley.

3.6 ESTIMATION OF MIGRATION RATES AND DISPERSAL RANGE OF *NOTHOFAGUS*

The rate of migration of tree species has been estimated by direct observation over a period of time (Griggs, 1946), by quantitative analysis of the population age profile at the edge of the species' range (Leak & Graber, 1974) and from dated appearances in the fossil record at a number of widely spaced localities (Davis, 1976).

The New Zealand fossil record is generally inadequate to obtain unequivocal estimates of tree or forest migration rates, although a series of three dated appearances of *Nothofagus* at different locations in and adjoining the study area was used to estimate migration rates for *Nothofagus* in this area. The assumptions used in the estimation are described in section 4.7.

The estimation of rates of marginal spread from the age

profiles of the *Nothofagus* populations at their boundaries is based on the observation that the canopy tree forming the boundary is generally younger than the next canopy tree away from the boundary, and that a seedling, sapling or subcanopy tree is generally established beyond the boundary canopy tree.

In successive transects across the boundary, pairs of individuals of different age were chosen that appeared to represent successful dispersal events in which the boundary is extended by the establishment of seedlings in a canopy gap adjacent to the canopy tree forming the boundary. The method is illustrated in Figure 5. Closely-spaced clumps of trees of apparently similar age, and cases where the parent tree was not evident, (for example, where more than one potential parent tree was present) were avoided. Only established seedlings greater than 25 cm in height and growing in a canopy gap were included in the samples. Inter-tree distances d_1 and d_2 were measured along the ground by a tape measure, and the ages a, b and c estimated from stem sections in the case of seedlings, saplings and small trees, or increment cores in the case of larger trees, see section 3.10. Some larger trees could not be aged by this method because of decayed trunk centres and were not included in the samples. The distance d_2 was measured to the furthest established seedling away from the boundary tree or, where larger individuals were present, to the furthest sapling or pole. Additional estimates of d_2 were made without estimating ages. At each measurement of d_2, the horizontal projection of the canopy of the boundary tree was estimated to the nearest 0.2 m. The limits of the canopy above the tape measure laid out to measure the distance d_2 were determined by sighting vertically by eye while standing on the tape measure.

Rates of marginal spread were obtained from the following formulae:

$$\text{rate of spread} = \frac{d1}{\text{age a - age b}} \; ; \quad = \frac{d_2}{\text{age b - age c}} \quad \text{(m/year)}$$

Three, undisturbed sections of the beech forest boundary, each approximately 200-400 m long, were sampled in Stands 3, 4 and 10 (see Table 4). The adjoining community in Stands 3 and 4 was

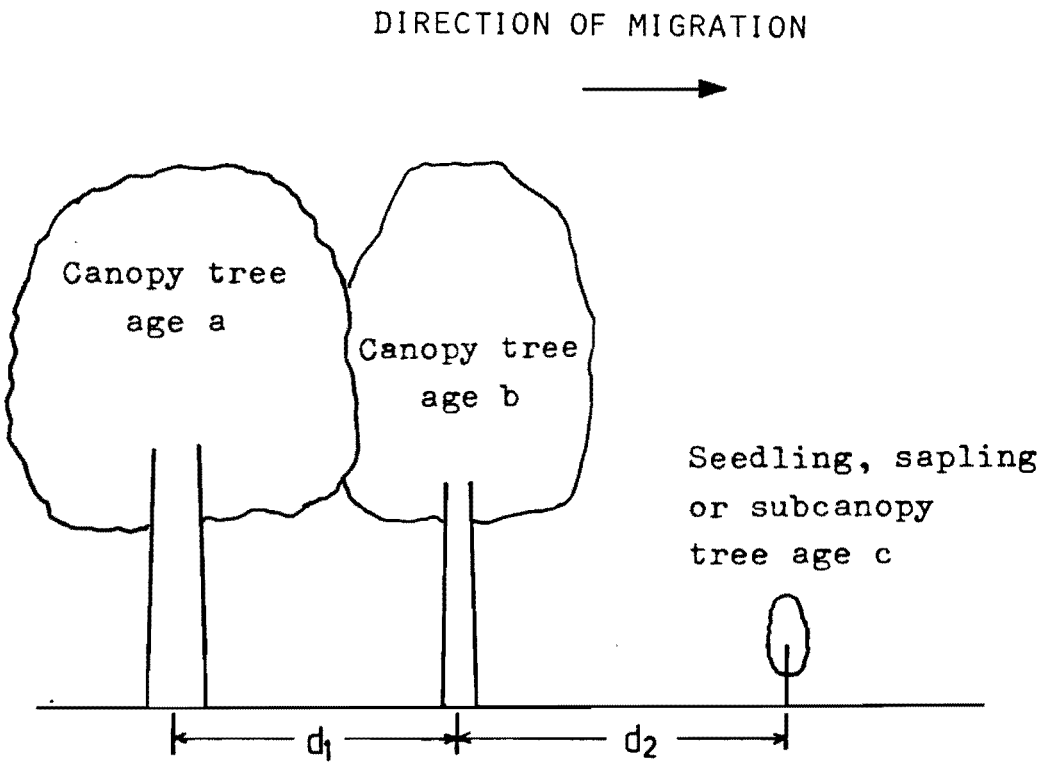


Figure 5. Generalised age profile at the beech forest boundary showing measurements used to estimate migration rates.

podocarp-hardwood forest dominated by *Dacrydium cupressinum, Metrosideros umbellata, Weinmannia racemosa* and *Quintinia acutifolia*. In Stand 10 the adjoining community was low subalpine scrubland dominated by *Olearia colensoi, Dacrophyllum longifolium* and *Dacrydium biforme* with some patches of tussock grassland.

3.7 POSITION OF THE BEECH FOREST BOUNDARY

The position of the beech forest boundary was examined in relation to site, soil, floristic and climatic variation within north Westland. Information on site variation was obtained using topographical maps (NZMSI, scale 1:63 360) and field reconnaissance; information on soil variation from published maps of varying scales (Gibbs *et al.*, 1950; N.Z. Soil Bureau, 1968; Mew, 1980); information on species distribution from published and unpublished records (Allan, 1961; Wardle, 1980c; C.J. Burrows, pers. comm.) and from personal observations; and information on climate variation from published accounts of regional climate (Garnier, 1958; Coulter, 1973; N.Z. Meteorological Service records, pers. comm. 1979).

3.8 DELINEATION OF LIFE STAGES

For the purposes of this study populations are subdivided into five life stages on the basis of the heights and positions of individuals in the forest subcanopy. The stages recognised are: (1) small seedlings - less than 7.5 cm tall, (2) large seedlings - from 7.5 cm to 100 cm tall, (3) saplings - from 1 m tall to 6 m tall, (4) poles - from 6 m tall up to the height of the canopy, (5) canopy trees - reaching the canopy or emergent from it.

The 7.5 cm height limit generally corresponds with a rapid decline in seedling frequencies with increasing height. The 1m and 6m limits are essentially arbitrary and were chosen for methodological reasons. Saplings and poles are not distinguished as separate stages in frequency sampling.

3.9 POPULATION SIZE STRUCTURES

The frequencies of small seedlings, large seedlings, saplings and poles and canopy trees of the major canopy tree species were measured in Stands 1,2,3,5,and 9 (see Table 4). The frequencies were then combined to produce complete population size structures. The primary aim of this sampling was to provide data on population size structures. Different sampling techniques were applied to the

different life stages in accordance with the frequencies of the various stages. These are described below. Regular sampling was used for greated efficiency in laying out quadrats.

Small seedlings

Seedling numbers were counted in square 1 m^2 quadrats placed at regular intervals of approximately 4 m on parallel transects about 30 m apart throughout each stand. Transects were a minimum of 100 m long and, where appropriate, were located at right angles to ridge crests. Sampling continued until the estimates of mean seedling density stabilised. This required a minimum of 120 quadrats in each stand.

Large seedlings

Seedling numbers were assessed in rectangular 10 x 15 m or 30 x 6 m quadrats placed within the quadrats used for saplings, poles and canopy trees. Quadrats were established by laying out tape measures along the ground surface. Right angles were obtained in the corner of the quadrats with the assistance of a sighting device which was held vertically in the corner and used to determine the directions along which the tape measure was laid out. A systematic search was made for seedlings within each quadrat with care being taken to search through any undergrowth. Details of sample sizes in each stand are given in Table 5.

Saplings, poles and canopy trees

Quadrats of variable size, usually 40 x 30 m, were laid out with tape measures using the technique described above. Pairs of contiguous quadrats were extended down both sides of a ridge, using the ridge crest as a mid-line. Successive pairs of quadrats were located at 80 to 100 m intervals along ridges and side ridges. In Stand 1, the pairs of quadrats were contiguous. The total areas sampled in each stand are shown in Table 5.

Table 5: Frequency sampling methods - total areas sampled. (Number of quadrats shown in brackets, where appropriate.)

	Large seedlings	Saplings and poles; Canopy trees
Stand 1	8 250 m^2 (55)	3.45 ha
Stand 2	10 800 m^2 (72)	1.08 ha
Stand 3c	2 160 m^2 (12)	1.03 ha
Stand 9	2 340 m^2 (13)	1.50 ha
Stand 5	1 800 m^2 (10)	1.08 ha

The data for diameter and height frequency distributions of saplings, poles and canopy trees were obtained during enumeration of quadrats in Stands 1, 2, 3c, 5 and 9 and by plotless sampling in Stands 4, 6 and 7. In plotless sampling the stand was covered systematically to ensure that all individuals were located. Stem circumferences were measured to the nearest cm using a measure extended around the stem at breast height (1.3 m above the ground approximately, taken from the uphill side of the stem where appropriate). The height of the individual in relation to the adjoining trees was noted and, in the case of rimu saplings and poles, the height of the individual to the nearest 0.5 m was estimated using 2 m measuring rods or a "Suunto" Hypsometer for the taller poles. Stem circumference measurements were converted to diameter measurements and grouped into 10 cm size classes.

3.10 ESTIMATION OF INDIVIDUAL AGES AND AGE STRUCTURES

The ages of individuals in each life stage were estimated by counting annual growth rings in transverse stem sections or stem increment cores.

In all species the growth rings are distinct to indistinct and appear to be annual rings, at least in rimu (Franklin, 1969; Jansen & Wardle, 1971), rata (Wardle, 1971b), kamahi (Wardle, 1966) and the *Nothofagus* species (Franklin, 1965a; Wardle, 1967). Discontinuous false rings which are fainter than adjoining growth rings were observed in parts of the stem sections of all species and were associated with widely spaced rings. Irregular radial growth also occurs in all species. The growth rings of rata were the most indistinct and were generally difficult to count.

Stem sections of all species were collected from living seedlings, saplings and poles in undisturbed forest and sections of rimu, miro, rata, *Quintinia* and kamahi from the stumps of felled poles and canopy trees in adjoining, recently logged areas within the study stands. Canopy trees of *Nothofagus* were sampled using stem increment cores. These were taken at a height of 50 to 80 cm above the ground. Cores passing more than 5 cm from the centre of the stem were not used. If necessary, more than one core was taken on different radii until a suitable core was obtained. Some of the larger trees could not be sampled because

of rotten stem centres. Stem sections of rata were difficult to obtain because few trees had been felled during logging.

Counting of growth rings

For small seedlings thin, basal stem sections were cut by hand with razor blades and examined at X60 and X100 magnification with a compound microscope. Growth rings were generally difficult to identify and most ring counts in the 5-10 ring range had an uncertainty of ±2 rings.

For larger individuals stem sections up to 10 cm thick were cut from the base of the stem (usually about 20 cm above the ground).

Stem sections were prepared firstly with a mechanical planer, then with a portable belt sander and finally with hand sanding on selected segments using one or two grades of sandpaper. Cores were placed in grooves cut in a wooden block and then prepared using sandpaper.

Ring counting was done without magnification where the rings were widely spaced and with a binocular microscope (X6 to X10) on the remainder of the section. The section was covered with a thin film of water to improve the clarity of growth rings. Growth rings were counted and marked off in groups of ten. The width of each group of ten rings was recorded to the nearest 0.5 mm. Faint, partial rings, assumed to be false, were excluded from the ring counts.

The accuracy of age estimates from large rimu stem sections was found to be within 2% of the mean estimate in a sample of six sections using two different radii and observers. The accuracy of age estimates from cores taken from large *Nothofagus* trees was found to be within 5% of the mean estimate in a sample of eight cores taken from four trees. An allowance was made in the age estimates for the time required to reach the height at which the section was taken. This was obtained from the age-height relationship for seedlings (section 4.11.5). The age estimates had an associated error of up to ±10 years from this allowance.

Estimation of age structure

Rimu stem sections were sampled from recently logged (clearfelled) areas of approximately 5 ha in Stand 1 (Callaghans Ridge) and 2 ha in Stand 6 (Notown) in 1977 and 1978, and age estimates were made from them. An attempt was made to sample all stems greater than 1 m in height. However, stems smaller than

5 m in height were difficult to find amongst logging debris and would have been undersampled. Consequently a minimum size limit of 5 m was used in deriving direct age estimates. This was found to correspond to an age limit of about 100 years. Some stem sections were unusable because of damage caused by tree felling.

An age structure for all individuals greater than 1 m tall (i.e. all saplings, poles and canopy trees) was derived from age estimates for trees greater than 5 m tall and, for individuals in the 1 to 5m height range (c. 25 to 100 years old), indirectly from the combined size-frequency distribution for Stands 1 and 6 (Fig. 29) so that the ratio of subcanopy to canopy trees in the population (0.39) was maintained.

The rimu stem sections have been stored in the Botany Department, University of Canterbury.

3.11 ESTIMATION OF GERMINATION, GROWTH AND MORTALITY RATES

Small seedlings (less than 7.5 cm tall)

The early establishment, outgrowth and mortality rates of small seedlings were monitored over a period of two to three years in permanent quadrats. A total of 148 1 m^2 quadrats were established in podocarp-hardwood and beech-podocarp forest in Stands 3, 4 and 5 during September and October 1974 and 1975 (Table 6). Quadrats were established on four different types of microsite: 'ground, under canopy'; 'log, canopy gap'; 'shrub layer, canopy gap'; and 'ground canopy gap'. 'Ground' and 'shrub' refer to quadrats established on the ground surface without and with a dense overhanging shrub layer respectively. 'Log' refers to quadrats established on fallen logs which were in a state of decomposition and supporting epiphytic plant life. Quadrats on the ground and on shrub microsites were square, those on fallen logs were rectangular with a minimum width of 0.25 m. Quadrats in canopy gaps were located beneath canopy openings caused by the death of one or more canopy trees and greater than about 3 m in diameter. Quadrats were placed in groups of four throughout an area of about 2 ha within each stand. Each group of four contained one of each type of microsite with all three of the canopy gap microsite quadrats together in the same gap. Half of the quadrats were placed in podocarp-hardwood forest and half

Table 6: Details of permanent quadrats established to monitor small seedling population dynamics.

Stand[1]	Year of quadrat establishment	Site	Beech species present
3A	1974	terrace	hard
3B	1975	terrace	hard
3C	1974	hill slopes	hard
4A	1975	hill slopes	hard
4B	1975	hill slopes	red
5	1974	hill slopes	red

[1] see Table 4 for locations and other details.

3A and 3B; 3C and 4A and 5 and 4B are replicate sets of quadrats established in consecutive years.

in beech-podocarp forest. There were 24 quadrats in each stand with the exception of Stand 3A where there was an additional group of four quadrats in podocarp-hardwood forest.

The positions of all seedlings of rimu, miro, rata, hard beech and red beech in the quadrats were recorded by the use of regular co-ordinates and stainless steel wire segments pressed into the ground and looped around the stems of the seedlings. Seedlings were measured each year from 1975 to 1977 during late winter (September to early October) when surviving seedlings and newly-established seedlings were located and tagged. The number of seedlings which had grown taller than 7.5 cm and the number of seedlings which had died back to less than 7.5 cm in the preceding year were also recorded. Observations were made concurrently on the possible causes of seedling mortality.

The following parameters were calculated for the seedling populations:

(i) early establishment rate - the number of newly-established seedlings recorded each year.

(2) mortality rate - the numbers of dead seedlings as a proportion of the total seedling numbers recorded in the previous year.

(3) net outgrowth rate - the numbers of seedlings growing taller than 7.5 cm subtracted by the number of seedlings dying back to less than 7.5 cm in height in each year of measurement.

For the small seedling populations the early establishment rate can be regarded as the rate of input into the population, and the mortality and net outgrowth rates combined as the rate of output from the population.

Large seedlings (7.5 - 100 cm tall)

The growth and survival rates of large seedlings were estimated from a permanently-tagged sample over a period of two to three years. Seedlings were tagged with numbered aluminium strips attached to the stem by stainless steel wire. Tagged seedlings were located throughout the areas occupied by permanent quadrats (see previous section) and assessed for growth and mortality at the same time of year. Tagged seedlings were placed within and adjoining the canopy gaps in which permanent quadrats were located, and in additional canopy gaps of the same minimum size and adjoining areas as required. For populations with high densities an attempt

was made to have tagged seedlings distributed at regular intervals. The heights of the main shoot of tagged seedlings to the nearest 0.5 cm and the number of dead tagged seedlings were noted at each measurement. Observations were made concurrently on the possible causes of mortality. Tagged seedlings were placed in approximately equal numbers in four different types of microsite: within canopy gaps, on logs; within canopy gaps, on the ground; under a canopy, on logs; under a canopy, on the ground. The classification of microsite types is the same used for permanent quadrats (previous section) except that microsites with an overhanging shrub layer are included in the 'on the ground' category. The four microsite types cover all seedling occurrences with the exception of seedlings epiphytic on tree trunks. Seedlings of rimu, miro and rata were tagged in both beech-podocarp and podocarp-hardwood forest in approximately equal numbers. The allocation of tagged seedlings in the study stands is shown in Table 7 (see also Table 6 for additional details).

Table 7: Initial numbers of tagged seedlings in study stands

Stand	Species				
	Rimu	Miro	Rata	Hard beech	Red beech
3A	79	97	80	80	-
3B	80	100	80	80	-
3C	77	-	80	80	-
4A	80	-	80	80	-
4B	80	-	80	-	80
5	80	-	80	-	80
Total no:	476	197	480	320	160

When dead seedlings were encountered during remeasurement, a nearby replacement seedling was tagged wherever possible. A few seedlings could not be relocated during measurement and were not therefore included in the analyses. In Stand 5 goat browsing caused a higher than usual mortality of the large tagged seedlings

of rimu, rata and red beech. As browsing pressure from goats was not present in the other stands, the mortality results from Stand 5 were not included in the analysis.

Rimu saplings, poles and canopy trees

Mortality rates were estimated by two methods:

Method 1: Permanently marked plots in which the positions and sizes of all rimu saplings, poles and canopy trees were recorded were established in Stands 1 and 3C. The plots cover areas of 3.45 ha in Stand 1 (podocarp-hardwood forest) and 1.125 ha in Stand 3C (0.630 ha in podocarp-hardwood forest and o.495 ha in beech-podocarp forest). The plots were established in 1975 and re-measured in 1978. Mortality rates were derived directly from the numbers of individuals dying during the period of observation.

The two permanent plots were established for the long-term monitoring of population dynamics. The plots have been registered with the N.Z. Forest Service, Westland Conservancy, Hokitika, as Westland Field Experiments 284 and 285 (G.P.S. Allan, Pers. comm., 1980). Details of the plot locations and boundary markings, together with a description of the experimental purpose, have been deposited with the Forest Service.

Method 2: In an attempt to avoid the limitations of a short period of observation inherent in Method 1, an alternative method of assessing the mortality rate was used.

All live and dead rimu canopy trees were censused within several areas. A total of 494 live and 47 dead trees were counted in a total area of about 20 ha within and around Stands 1 and 2. Only canopy trees were included in this method because of the difficulty of locating smaller dead trees and the likely differences in decay rates between large and small trees. All dead trees clearly identifiable as rimu (verified by the presence of intact bark) were included in the census. Trees in a more advanced state of decay, which could have been confused with miro *(Podocarpus ferrugineus)* or other species, were therefore excluded.

The period for canopy trees to decay beyond a recognisable state was estimated by dating the time of death, where possible. This was done in two ways. In the case of windthrown trees, the time of formation of scars on the trunks of adjoining trees (usually *Quintinia* and kamahi) caused by the falling tree were estimated from growth rings in stem sections around the scar.

In other cases, the ages of *Quintinia* and kamahi saplings and seedlings growing in thickets around the base of a standing or fallen dead tree in apparent response to a large opening in the canopy were estimated (see section 3.10).

There are several uncertainties in this method. The decay rate of individual trees may vary considerably between trees which remain standing and those which have fallen at death. The trunks of some trees have partially decayed before death, although most trees had completely sound trunks at the time of death. The decay time determined from the time of scar formation on adjoining trees would be an underestimate if the rimu tree had remained standing for a number of years before falling. A delay in the colonization of the area around a dead canopy tree by hardwood seedlings would also lead to an underestimation of the decay time.

Of the eighteen estimates of the decay time that were possible, all estimates were less than 20±6 years for decay to to an unrecognisable condition except for three estimates of 26±5 years, 45±8 years and 54±5 years. This indicates a range of mean decay time from about 20 to 50 years. This range is used to obtain a range of estimates of mortality rate.

During the census of live trees, observations were made on the possible causes of death and the direction of fall of dead trees.

3.12 GROWING POSITIONS OF RIMU LARGE SEEDLINGS, SAPLINGS AND POLES

Groups or individuals of large rimu seedlings, saplings and poles in podocarp-hardwood forest in parts of Stand 2 destined for logging, together with the adjoining canopy trees of *Quintinia*, kamahi, *Phyllocladus alpinus* and rata, were sampled for age estimates using the methods described above. Eight separate groups of stems were sampled. The relative heights and distances apart of the young rimu individuals and adjoining trees and shrubs and the species composition of the overhead canopy were also noted. Supplementary observations were made throughout the study area (section 3.1). In beech-podocarp forest on better-drained sites rimu regeneration was too infrequent to enable detailed examination.

CHAPTER FOUR

RESULTS

4.1 GENERAL PATTERNS OF *NOTHOFAGUS* DISTRIBUTION IN NORTH WESTLAND

Nothofagus occupies much of the northern part of the Westland region, forming extensive forests of the pure beech and beech-podocarp types. Within these forests, one or more of the four *Nothofagus* species generally comprise the predominant canopy cover. Few of the available growing sites between sea level and timberline are not occupied by at least one of the species.

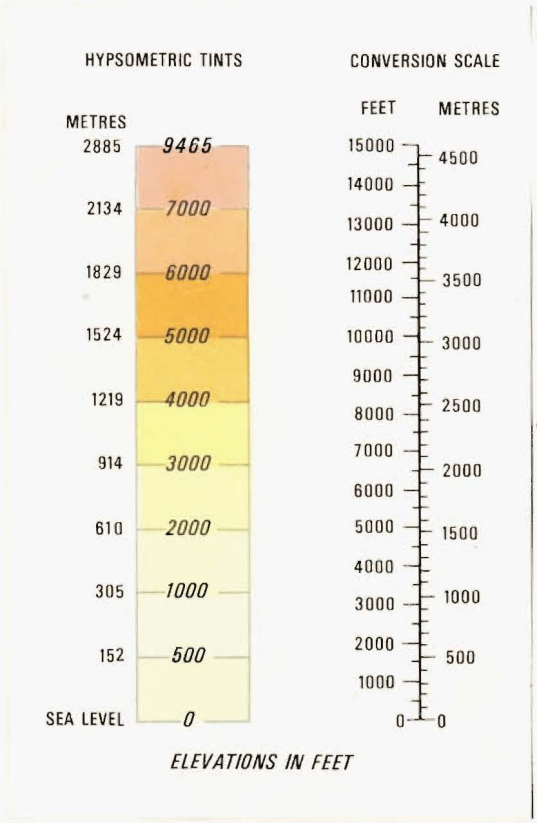
The north Westland beech forests have sharply-defined southern limits of distribution between Greymouth and Harpers Pass. The southern boundary of *Nothofagus* forms an irregular line oriented in an east to west direction (Figure 6). One prominent feature of the boundary is the presence of long, narrow protusions of beech forest along river valleys and lower valley sides, or occasionally across glacial outwash terraces. Elsewhere, the boundary crosses low altitude hill country and the flanks of the southern Paparoa Range. Beyond the main area of beech forest, and largely in close proximity to it, there are numerous pockets or 'outliers' of beech forest within a matrix of podocarp-hardwood forest or sub-alpine scrubland. These outliers range in size from single individuals to stands of up to several hundred hectares in area. A separate, large area of distribution is located in the upper Taramakau catchment and closely adjoins beech forest to the east of the Main Divide.

In the vicinity of the southern limits of distribution there are a number of areas of podocarp-hardwood forest surrounded completely by beech forest. These are termed podocarp-hardwood forest enclaves. Most enclaves occupy hill slopes and are enclosed by beech forest occupying low ground. Three large enclaves of podocarp-hardwood forest are found on largely mid-slope positions in the southern Paparoa Range. Here, beech forest occupies the lower slopes and also a zone of high altitude sites extending downwards from timberline.

Figure 6. Limits of distribution of Nothofagus forest in north Westland and adjoining areas of the Southern Alps (1 : 500 000).
The study area is the outlined hexagon.
A more detailed map of boundaries, including the distribution of small outlier stands not shown here is presented in Figures 8, 9, 10, 11 and 12.

Beech forest areas are shaded in red

(N.B. The correct position of Totara flat is shown in Fig. 4)




0 10 km
71°
42°
172°
43°
Cape Foulwind
Nine Mile Beach
Buller River
Charleston
Seal I
Kaipakati Point
Perpendicular Point
Dolomite Point
Punakaiki
PAPAROA RANGE
Barrytown
Rapahoe
Point Elizabeth
Cobden
GREYMOUTH
Karoro
Boddytown
Paroa
Gladstone
Rutherglen
Cameron
Kumara Junction
Kumara
Arahura
Kaniere
Kokatahi
Whitiranga
Runanga
Taylorville
Dobson
Blackball
Ngahere
Stillwater
Totara Flat
Mt Faraday
Mewheraiti
Hukarere
Ikamatua
Moana
Lake Brunner
Arnold River
Grey River
Taramakau River
Otira
Lake Kaniere
Styx River
Mt Rolleston
Arthur's Pass
Browning Pass
Fairdown
Sergeants Hill
Inangahua Junction
Orikaka River
Blackwater River
Inangahua River
Reefton
Waiotahi River
Waiotahi River
Rough River
Nelson Creek
Lake Christabel
Lake Haupiri
Haupiri
Kopara
Lake Poerua
Otira River
Taipo River
Arthur River
Totara River
Clarke R
Upper Grey R
Murchison
Buller River
Matakitaki River
Maruia River
Deception River
Deepdale River
Paenga
Mt Mentell
Mt Victoria
Cronadun
Maruia
Mt Albert
Springs Junction
Mt Technical
Mt Rapeses
Mt Hochstetter
Robinson River
Amuri Pass
Waiheke River
Doubtful River
Mt Alex
Hope Pass
Hope River
Kakapo Brook
Mt Longfellow
Lake Sumner
Harper Pass
Mons Sex Millia
Lewis Pass
Boyle River
Mt Jervis
Tutaki
Rotoroa
Manales River
Matakitaki River
Gibbons River
Glenroy River
Spenser Mts
BRUNNER RANGE
SOUTHERN ALPS
TARAPUNGA RANGE
BEECH FOREST BOUNDARY
BEECH TIMBERLINE

There are particular sites within the north Westland beech forest area where *Nothofagus* is absent or sparsely distributed. The most conspicuous examples are close to the coastline where exposed sites are occupied by low hardwood forest, scrubland or podocarp-hardwood forest, and *Nothofagus* is confined to sheltered gullies and higher slopes. *Nothofagus* is also scarce on sections of the broad alluvial plains, as for example near Barrytown and around Totara Flat in the Grey River valley. The north faces of the prominent limestone ridges 7 km to the east of Punakaiki and portions of the coastal limestone plateaux to the north of Punakaiki are further sites where *Nothofagus* is absent or scarce.

The beech forest timberline is anomalously depressed by up to 300 m in altitude along the western flank of the south-western arm of the Brunner Range (Figure 6). In this area both *N. menziesii* and *N. solandri* var. *cliffortioides* are missing from part of their normal range, or are present only as small stands (Holloway, 1954).

4.2 *NOTHOFAGUS* DISTRIBUTION IN THE STUDY AREA

The distribution patterns of the *Nothofagus* species in the study area are described in turn for ten districts which, between them include all known occurrences of *Nothofagus* in the study area. These descriptions should be read in conjunction with Figures 8, 9, 10, 11 and 12 which detail the position of the beech forest boundary and the location of outliers. The overlap between Figures 8-12 and the districts is shown in Figure 7.

4.2.1 Southern Paparoa Range (Figs 8 & 9)

Along the coastal section of the Range, the beech forest boundary forms an irregular line within several hundred metres to 2 km of the coastline. The boundary tends to extend furthermost downwards on ridges, and comes closest to the coastline at sheltered places on the marine benches south of Greigs.

Nothofagus truncata is the predominant species on hill slopes; *N. fusca* and *N. menziesii* are also present on hill country in the vicinity of Barrytown, and *N. menziesii* and *N. solandri* var. *cliffortioides* are present on the coal measures to the south of Ten Mile Creek. *N. solandri* is the predominant species on lower slopes and marine benches between Greigs and Rapahoe. *N. fusca* appears to be absent from the coal measures.

Beech forest forms the timberline on the western side of the Range, but *Nothofagus* is absent from some sections of the eastern timberline. To the north of Mt Watson the timberline occurs from 910 to 1070 m a.s.l. and *N. menziesii* is the only *Nothofagus* species at timberline. To the south, in the vicinity of Mt Davy and Sewell Peak, the beech timberline is generally lower (550 to 1010 m a.s.l.) and is formed by stunted trees of *N. solandri* var. *cliffortioides* and *N. menziesii*. In this area Brunner Coal Measures are the parent material in contrast to the greywacke parent material in the north (Bowen, 1964).

North of Mt Watson, *N. fusca, N. truncata* and *N. solandri* var. *cliffortioides* (the fuscoid group of species) are absent from an altitudinal zone of 300-450 m below timberline. *N. fusca* grows to a higher altitude than the other species in steep-sided valleys on the western side of the Range. This pattern continues to the north of the study area (see Fig 14).

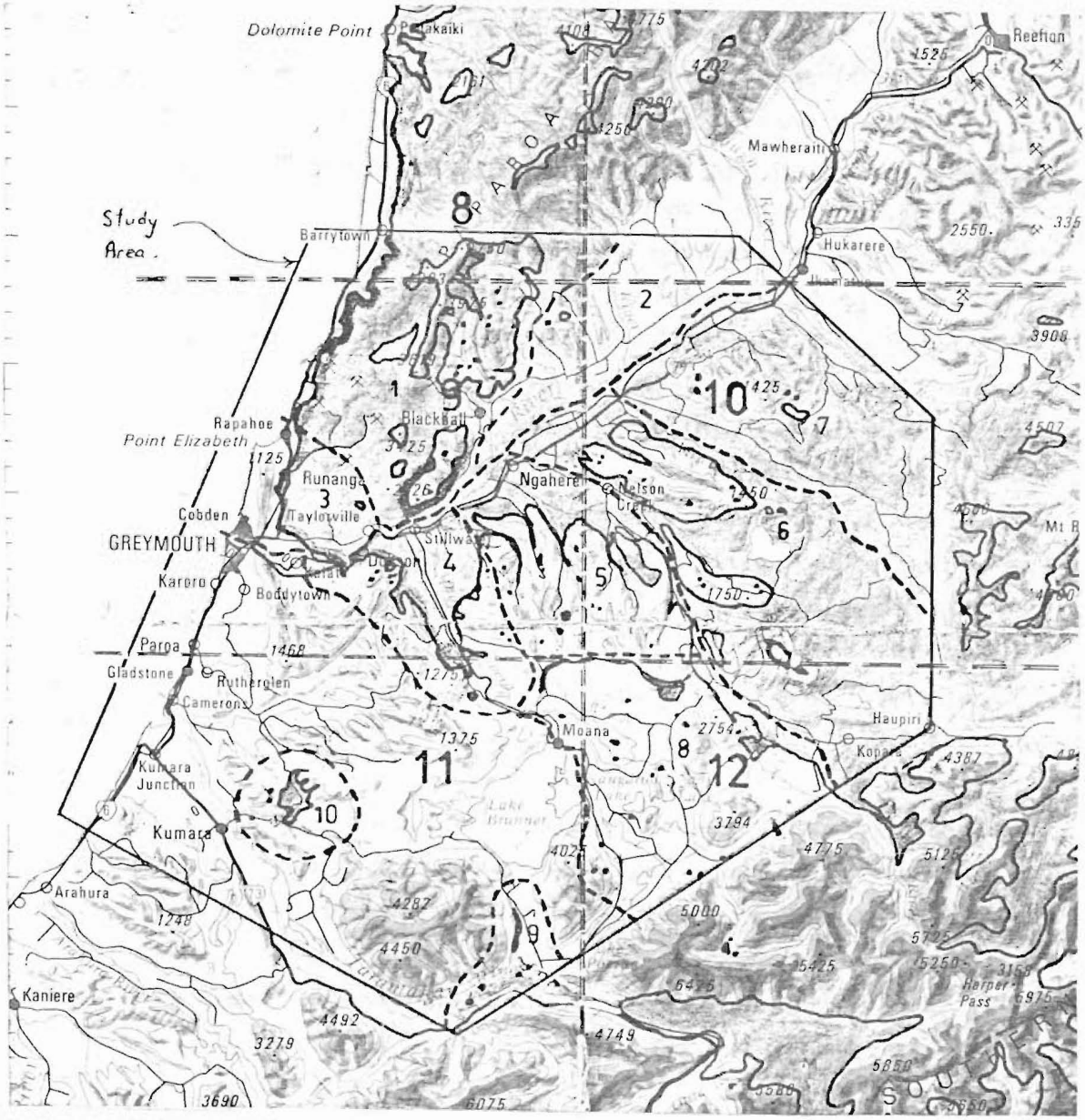


Figure 7: Districts within the study area used to describe Nothofagus distributions.
Small numbers 1 to 10 refer to the districts, which are outlined by heavy dashes.
Large numbers refer to figures of the same number.
Areas covered by Figs 8 to 12 are outlined by double dashes.

N. solandri var. *cliffortioides* is normally present in the upland forests and at timberline elsewhere in north Westland.

A large enclave (520 ha) of podocarp-hardwood forest extends along the upper reaches of Ten Mile Creek on the western side of the Range.

On the eastern side there are two large and two small enclaves of podocarp-hardwood forest. The largest (4500 ha) includes the upper catchments of Blackball, Roaring Meg and Moonlight Creeks and other smaller creeks. The upper boundaries of this enclave are formed by timberline or upland areas of *N. menziesii* dominant forest; the lower boundaries, along the foot of the Range, are formed by the four *Nothofagus* species. In places beech forest protrudes into the enclave along valleys. Examples of this pattern are found in the lower and upper reaches of Blackball and Roaring Meg Creeks. Outliers are frequent in the upland forests of this enclave and occupy substantial areas. These outliers all comprise *N. menziesii*. Small colonies and single individuals of this species are frequent in parts of the subalpine scrubland and tussock grassland areas. The small *N. menziesii* outliers are generally circular in shape. In the centre of some outliers there is a single , large, heavily-branched *N. menziesii* tree surrounded by a dense stand of smaller trees. Around the perimeter of the stand is a further band of saplings or smaller trees. In the lowland forests within the enclave, outliers are composed of *N. menziesii*, especially those found on stream banks and lower valley sides along Blackball Creek, or *N. fusca* near the lower margins of the enclave, for example, in the vicinity of Blackball Creek and Fitzgerald Creek.

Another large podocarp-hardwood forest enclave of 1300 ha extends along the mid-slopes of the Range to the east of Mt Davy and south-west of Blackball. The upper boundaries of this enclave are formed by *N. menziesii, N. fusca* and *N. solandri* and the lower boundaries by *N. fusca, N. truncata* and *N. solandri* (except in the valley of Blackwater Creek where *N. menziesii* forms the boundary). Seven outliers are present within the enclave.

Between the two larger enclaves beech forest extends across a low point on the Range near Roa. Two small enclaves of podocarp-hardwood forest are located to the west of Blackball (map references S44/899985, 879978).

4.2.2 Big River (Figs 9 and 10)

Five small enclaves of podocarp-hardwood forest ranging in size from 0.6 ha to 50 ha occupy ridge crests and upper slopes on the low altitude hill country between Moonlight and Caledonian Creeks. These have been heavily modified by logging. The four *Nothofagus* species are present throughout this district.

4.2.3 Runanga (Fig 9)

The beech forest boundary has been highly modified or removed in most of this district. In two places beech forest extends on to the lower inland flanks of the Rapahoe Range. At one place (map reference S44/765920) all four *Nothofagus* species are present near the boundary. In the vicinity of the lower reaches of Coal Creek the boundary is formed by *N. menziesii*.

N. fusca is absent from much of this district, being present only at the locality just mentioned above, along the banks of the Grey River and on the lower slopes of Sewell Peak. The other three species occur throughout.

There is one small podocarp-hardwood enclave on the lower western slopes of Sewell Peak.

4.2.4 Arnold River (Figs 9 and 11)

In this district the beech forest boundary extends from the poorly-drained alluvial terraces of the Grey River between Kaiata and Dobson, across the southern slopes of Mt Buckley and upstream along the Arnold River valley for a distance of 12.5 km. In places the boundary is confined to the banks or the flood plain of the Arnold River, but elsewhere beech forest extends on to low outwash terraces of the Loopline Formation. Small protrusions of the boundary are found along Maori Gully Creek, Piper Creek and other unnamed creeks. There is one small enclave of podocarp-hardwood forest on the south-western slopes of Mt Buckley (map reference S44/844883). Outliers containing *N. fusca* and *N. truncata* are common on hill slopes around Lisbon Creek and outliers containing *N. fusca* and presumed *N. fusca x N. solandri* hybrids occur along the small flood plain of Piper Creek. In other places beech forest outliers could have been removed by farming activities. One 10 ha outlier containing only *N. fusca* covers rolling hill country near Mallinsons Creek (map reference S51/913758).

N. menziesii has a restricted distribution in this district; the species is present only within 5 km of the Grey River on the slopes of Mt Buckley (an outlier to its main area of distribution), along the lower reaches of Stillwater Creek and the Arnold River and on low outwash terraces. The beech forest boundary is generally formed by *N, fusca* in admixture with *N. truncata* in some locations..

4.2.5 Mawhera (Figs 9 and 10)

Beech forest occupies most of the low ground around the periphery of the district leaving podocarp-hardwood forest on the dissected hill country and high outwash terraces in the central area. Protrusions of beech forest extend from the Grey River flood plain upstream along small side valleys, notably along Twelve Mile, Red Jacks and Dead Horse Creeks. These protrusions extend for up to 8 km. Another protrusion covers much of a high outwash terrace around Roaches, Graham and Cochrane Creeks. Narrow valleys such as Deadman Creek and Sunday Creek do not contain protrusions of beech forest.

Eighteen beech forest outliers were located on the central hill country and associated high terrace remnants. *N. fusca* is present in all but two outliers, *N. solandri* var. *cliffortioides* in the five outliers on outwash terraces, and *N. truncata* in five others. *N. menziesii* is absent from all of these outliers and much of the remaining beech forest. It is found on lower slopes along the edge of the Grey River flood plain.

N. fusca is present along all of the beech forest boundary; *N. truncata* or *N. solandri* var. *cliffortioides* are present at the boundary in a few places but are otherwise within several hundred metres of the boundary.

4.2.6 Hochstetter (Figs 10 and 12)

This district exhibits a distribution pattern similar to the Mawhera district; beech forest occupies the lower ground leaving large enclaves of podocarp-hardwood forest on the hill country and high terraces. There are four large enclaves (one centred around Callaghans Creek, one on Lake Hill Ridge, one on Granite Ridge 6 km south of Lake Hochstetter and one on outwash terraces near Findlay Creek) and 11 smaller enclaves in close proximity to them. Beech forest occupies hill country at the eastern and

north-eastern ends of the three largest enclaves. This pattern is illustrated for Lake Hill Ridge in Fig 23.

Long valley protrusions of beech forest are found along Callaghans Creek, German Gully and Gows Creek, and smaller protrusions are noticeable on many of the smaller streams, particularly when these are steep-sided with unstable banks. Examples are found on the streams on the south face of Lake Hill Ridge.

Outliers are found scattered throughout the enclaves. Most are *N. fusca* outliers located close to the main boundary on hill slopes and in gullies. The largest outlier (8.0 ha, map reference S45/102924), is found on the high terrace remnant between the sources of Callaghans and Gows Creeks. *N. fusca, N. truncata* and *N. solandri* var. *cliffortioides* are present and the outlier extends around the southern margins of an induced pakihi which occupies the centre of the terrace. Across the pakihi to the north-west is another smaller outlier which may have been connected with the larger outlier before the clearing of the pakihi area. Both outliers reach the terrace edges and extend for 50-100 m down the heads of deep gullies.

In most places *N. fusca* forms the boundary while *N. truncata* and *N. solandri* var. *cliffortioides* are found within a hundred metres of the boundary. The last named species forms the boundary on a poorly-drained intermediate terrace to the north-west of Lake Hochstetter.

N. Menziesii is present in the beech forests on the valley morainic country east of Lake Hochstetter (see Fig 14) but elsewhere only in two widely spaced outliers within beech forest, otherwise containing only the fuscoid group of species. One of these, of 0.25 ha, is on a high terrace near Gorgy Creek (map reference S45/077906) and the other, a large outlier, on the central part of Granite Ridge (map reference S52/174798). The other three species are present throughout the beech forests in this district, except at parts of the boundary as noted above.

4.2.7 Granville (Fig 10)

The only areas not occupied by beech forest in this district are two clusters of small podocarp-hardwood forest enclaves near Napoleon Hill and Kaka Hill. These enclaves, which range in size from

0.4 ha to 36.5 ha are all located on hill slopes, generally astride ridge crests.

The predominant species at the boundary is *N. fusca* but *N. truncata* is also present at the boundary in places, or is within 30 m of the boundary. *N. menziesii* is restricted to the rolling morainic country in the eastern part of the district, to the flood plain of the Grey River and to a series of 6 small outliers in the narrow flood plains of streams draining into the Grey River near Totara Flat. Two of these outliers have an elongate shape; they are widest near the upstream end with a long 'tail' extending downstream and gradually narrowing to a few individuals growing on the stream banks.

4.2.8 Moana-Bell Hill (Figs 11 and 12)

The main beech forest boundary runs at the foot of the northern slopes of Bell Hill, an isolated block of greywacke and argillite. On the eastern slopes of Bell Hill is a small outlier and a large protrusion of the main boundary. The Bell Hill mountain block is dissected by the headwaters of Deep Creek. A deeply-incised gully on the western slopes of the block contains a *N. fusca* outlier. This outlier is largely confined to the gully, but extends for about 40 m on to nearby slopes in one place. A single *N. fusca* tree is found on the talus far below the outlier.

The moraines and low outwash terraces between Bell Hill, the Mawhera hill country and Lake Brunner support scattered outliers of *N. fusca* or *N. fusca* with *N. solandri* var. *cliffortioides*. Forest clearance has been extensive in this area so some beech forest outliers may have been removed. Some outliers are associated with water courses, others are located on moraines or terraces well away from streams or rivers. For instance, the 9.3 ha *N. fusca* - *N. solandri* var. *cliffortioides* outlier immediately to the north north-west of Lady Lake and a much smaller *N. fusca* outlier to the north-west of the lake are situated on moraines of the Moana Formation (Gregg, 1964).

The Deep Creek outlier

This large (310 ha) outlier is shown on a separate map (Fig 13). The outlier covers an altitudinal range of 90 to 220 m a.s.l. It is mostly confined to the narrow alluvial flood

Figure 13. The Deep Creek beech forest outlier and its environs.

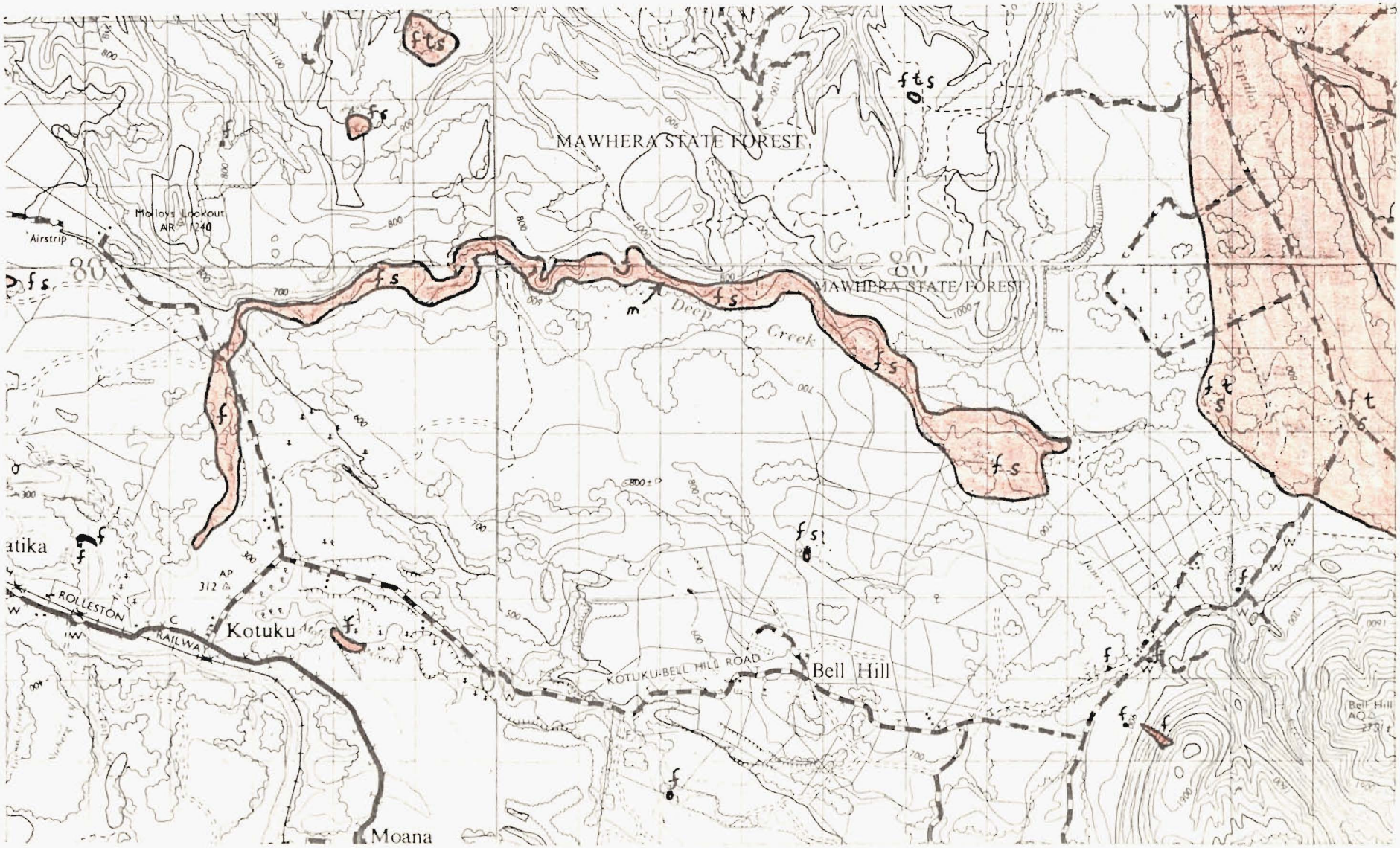
Beech forest

f *Nothofagus fusca*

t *N. truncata*

s *N. solandri* var *cliffortioides*

m *N. Menziesii*


MAWHERA STATE FOREST
MAWHERA STATE FOREST
Molloys Lookout
AR 1240
Airstrip
Deep Creek
ROLLESTON
RAILWAY
Kotuku
AP
312
KOTUKU-BELL HILL ROAD
Bell Hill
Moana
Bell Hill
AQ

plains of Deep Creek but extends on to the adjoining low outwash terrace particularly at its eastern end. The outlier is largely composed of *N. fusca* with small areas of *N. solandri* on the outwash terrace along the southern margins of the outlier. A small 0.1 ha stand of *N. menziesii* is located on the sloping terrace edge near the centre of the outlier. The outwash gravels occupied by part of the outlier are of the Loopline Formation (Gregg, 1964).

Four outliers are found on the north-eastern slopes of Mt Te Kinga. Unlike other outliers in the district, these outliers occupy stable, midslope or lower slope positions rather than steep-sided gullies (which are present on Te Kinga). These outliers together with the five outliers in the Rotomanu area, are composed of *N. fusca*, although presumed *N. fusca* X *N. truncata* hybrid trees are present in one of the Te Kinga outliers. The Rotomanu outliers occupy gully sides or alluvial sites on the banks of the Crooked River near its junction with Evans Creek.

4.2.9 Taramakau-Orangipuku (Fig 11)

Stands of *N. fusca* along the flood plain of the Taramakau River in this district are outliers to the large areas of distribution in the upper Taramakau catchment (see Fig 6 and section 4.3).

The elongate 20 ha outlier for 3.8 km along the banks of the Orangipuku River contains both *N. fusca* and *N. menziesii*. Forest clearance has probably reduced its size.

4.2.10 Blackwater Creek - Greenstone (Fig 11)

Beech forest in the district comprises the large Blackwater Creek outlier with its smaller satellite outliers.

The Blackwater Creek outlier covers about 360 ha at an altitudinal range of 60 to 170 m a.s.l. Most of the outlier is on a high outwash terrace of the Waimea and Cockeye Formations where the four *Nothofagus* species are present, but stands of *N. fusca* and *N. menziesii* also extend upstream and downstream along the deeply-incised gullies which form the tributaries of Blackwater Creek. Goldmining activity along the Greenstone River has presumably removed some of the outlier; two *N. fusca* trees 2.5 km downstream could represent an extension of the original stands into the Greenstone valley. A series of small outliers is found on the edge of the outwash terrace at the head of nearby

Big Fuchsia Creek (where the three fuscoid group species are present) and downstream along the banks of the creek as single *N. fusca* trees.

This outlier and its environs have been extensively modified by timber extraction and goldmining, although parts of its western boundary are only lightly modified.

No stands of beech forest are known in the remainder of the study area outside the ten districts described above.

4.2.11 Distributions of the individual *Nothofagus* species

The geographical distributions of *N. fusca*, *N. truncata* and *N. solandri* var. *cliffortioides* within the study area are substantially similar, except that *N. truncata* is absent from the vicinity of the Alpine Fault eastwards (Fig 14). Within the beech forest areas there are few places where any of these species are absent from their normal sites. The major areas where these species are absent are in a high altitude zone extending to approximately 300 to 450 m below timberline in the southern and central Paparoa Range and in parts of the Tutaekuri and Waitaki catchments in the Southern Alps (Fig 14). Silver beech *(Nothofagus menziesii)* occupies these areas and forms the timberline. Elsewhere *N. solandri* var. *cliffortioides* is also present near timberline.

Nothofagus menziesii has a more restricted distribution than the fuscoid group of species in the lowland forests of the Grey valley, being largely absent to the east and south of the Grey River up to the southern beech forest boundary (Fig 14). Nine small, isolated *N. menziesii* stands are located throughout the beech forests of this area (see sections 4.2.6 and 4.2.7). *N. menziesii* also occurs in three of the lowland beech forest outliers and in the Taramakau catchment. While *N. menziesii* is widespread in the upland beech forests to the east of the Grey valley, there are several noticeable gaps in its distribution, namely on the upper slopes of Mount Elliott and Mount Harata (Holloway, 1954). *N. fusca* forms the timberline at these locations.

The *Nothofagus* species present at the beech forest boundary within the study area are not generally those which normally occupy each type of site (cf. Table 3). *N. fusca* and its hybrids with *N. solandri* and *N. truncata* constitute most of the

Figure 14: *Nothofagus* species' distribution in north Westland and adjoining areas of Canterbury. (1 : 500 000).

KEY

fuscoid group species only present (*Nothofagus menziesii* absent).

N. menziesii only present.

fuscoid group species and *N. menziesii* present.

M — Extensive *N. menziesii* stands present. (In remainder of the Canterbury beech forests, cf. Fig 6, *N. fusca* and *N. solandri* only are present.)

m — Outliers of *N. menziesii*[1] (in north Westland).

• — Outliers comprising fuscoid species only.[1]

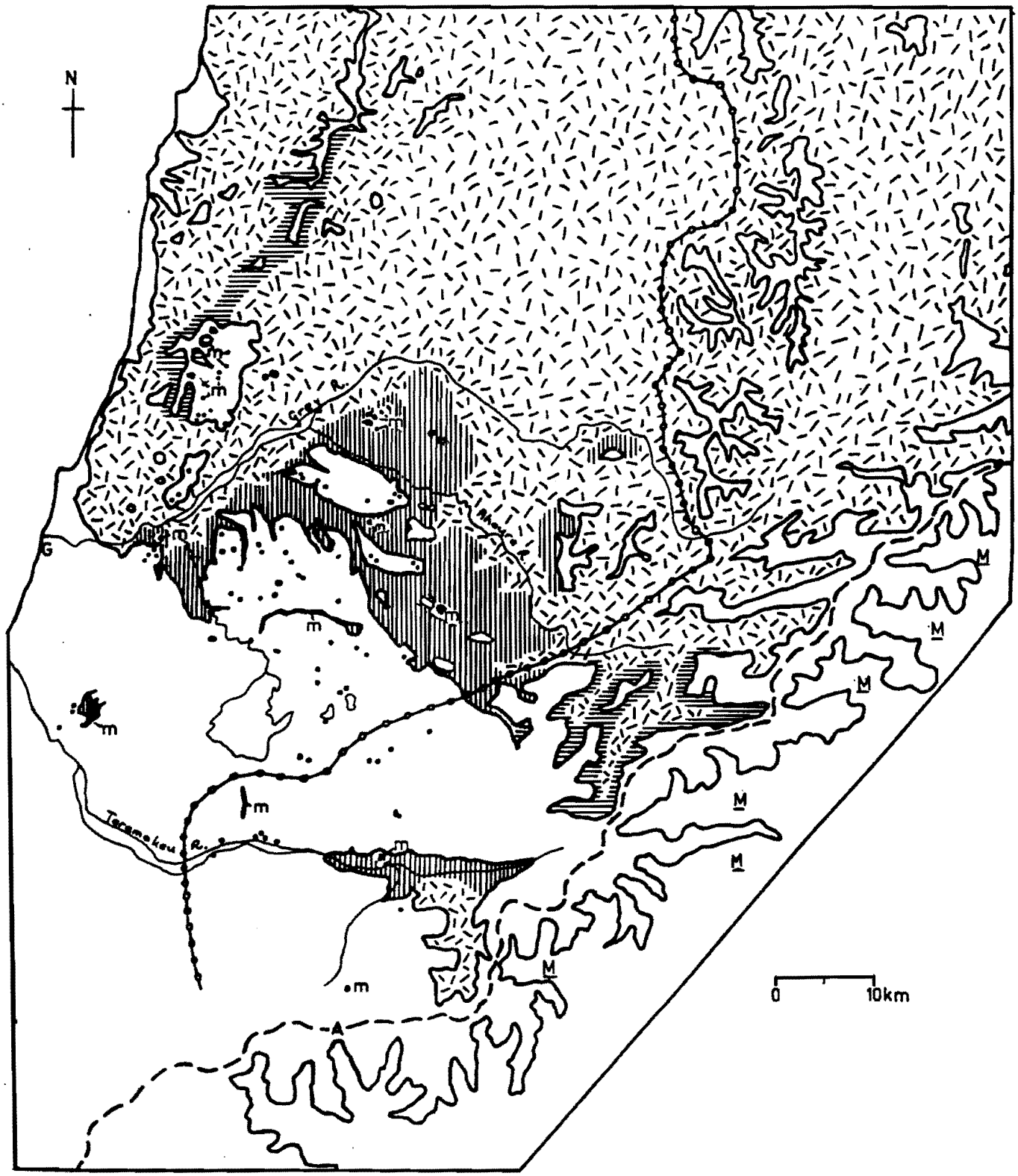
G — Greymouth.

A — Arthurs Pass.

Main Divide of Southern Alps.

Eastern limits of *N. truncata*.

[1] Detailed distributions of *N. menziesii* are shown in Figs 8 - 12.


N
G
m
M
Tarramoo
R.
A
0
10km

boundary in the lowland forests, although each of the other *Nothofagus* species may also be present at the boundary in limited areas. In these areas the boundary may be formed by *N. truncata* on ridge crests, *N. solandri* var. *cliffortioides* and *N. truncata* on terraces or by *N. menziesii* in valleys. The transition from pure *N. fusca* forest at the boundary to a mixed species forest takes place within a few hundred metres of the boundary. *N. menziesii*, however, may be absent for a much greater distance from the boundary (Fig 14). In contrast to the lowland situation, the beech forest boundary in the southern Paparoa Range is normally formed by *N. menziesii, with N. solandri* var. *cliffortioides* located up to several kilometres distant from the boundary.

Hybrids formed between the three species of the fuscoid group - *Nothofagus fusca, N. truncata* and *N. solandri* var.*cliffortioides* - are generally uncommon in the north Westland forests. However, an increased incidence of hybrid individuals was noted in the vicinity of the beech forest boundary, in the beech forest outliers and on disturbed sites such as logged areas.

4.3 *NOTHOFAGUS* DISTRIBUTION IN THE VICINITY OF THE STUDY AREA

4.3.1 East of the Alpine Fault

The beech forest of the upper Taramakau catchment (Fig 6 and Fig 12) is not an outlier to areas of distribution in north Westland but rather a separate area of distribution lying in close proximity to the beech forests of the Poulter catchment to the east of the Main Divide.

Nothofagus fusca, *N. solandri* var. *cliffortioides* and *N. menziesii* are present, with the latter two species being largely confined to the Otehake catchment and *N. fusca* extending further than the other species in the Taramakau Valley and in the lower section of the Otira Valley (Wardle & Hayward, 1970).

Both recent expansion of *N. fusca* and non-regenerating *N. fusca* boundary stands are evident in the Taramakau valley (Burrows & Greenland, 1979).

Riparian stands of *N. fusca* occur in Camp Creek catchment near Poerua (G.H. Stewart, pers. comm., 1980), and in the upper section of the Crooked River, see Fig 12. The four Crooked River stands cover in total 30 ha and are 3-7 km in a direct line from the closest area of *N. fusca* in the Taramakau valley.

4.3.2 Barrytown - Punakaiki (Fig 8)

Beech forest is absent from most coastal areas, including the Barrytown plain and exposed hill slopes bordering the plain and the coastline further north. *N. truncata* comes on to the edge of the plain at one place in the Waiwhero Scenic Reserve. Further gaps in the distribution occur on the north faces of the Waikori Ridge inland from Punakaiki and on large sections of the karst plateaux to the north of Punakaiki. The lower slopes of the narrow gorges of streams which dissect the plateaux also generally lack beech forest. A group of scattered, dead *N. fusca* trees with no seedlings nearby are present in podocarp-hardwood forest several hundred metres from beech forest at the crest of Waikori Ridge.

The four *Nothofagus* species are found throughout this area, although *N. solandri* var. *cliffortioides* appears to be absent from the crest of the Paparoa Range to as far north as Mt Priestly.

4.4 THE BEECH FOREST BOUNDARY

The boundary between *Nothofagus*-dominated and adjoining communities is in general sharply defined. Within the *Nothofagus* communities the *Nothofagus* species form a nearly continuous canopy in which other species are infrequent. Beyond the edge of the beech canopy at the boundary only occasional beech trees or small stands of trees are found, although clumps of beech seedlings and saplings are common in canopy gaps immediately adjacent to the canopy edge. An exception to this typical pattern is found where *N. menziesii* forms lower altitudinal limits at c 640 m a.s.l. on the eastern flanks of the southern Paparoa Range. Here the density of beech canopy trees gradually declines further into the podocarp-hardwood zone until only scattered trees and stands remain. The boundary in this case is poorly defined. A similar boundary is found at the coastal limits of *Nothofagus* north of Rapahoe.

The age and size structures of the beech populations generally show a transition across the boundary, changing from a young population at the edge to a mixed-age population away from the edge. Thus seedlings and saplings occur immediately beyond the limits of the beech canopy, small to medium sized trees usually form the canopy at the boundary, and large live and dead beech trees are further removed from the boundary. This general pattern is confirmed from many observations of undisturbed sections of the beech forest boundaries throughout the study area. In *Nothofagus* there is a sufficiently strong correlation between stem size and age (see section 4.10; Armstrong & Bussell, 1964; Ogden, 1978) for observed tree sizes to be interpreted in this way.

There are some exceptions to the general pattern. Some boundary trees are large rather than small to medium sized, and in some places trees of all sizes or predominantly larger trees form the boundary. Seedlings may be infrequent beyond the canopy edge in these cases. This pattern is found in the coastal boundaries north of Rapahoe, on the lower slopes of the Rapahoe Range, on the higher altitude sections of timberline north of Mt Watson and on the mid-slope *N. menziesii* boundary on the eastern flanks of the southern Paparoa Range. All species of *Nothofagus* are involved in this pattern. The only location where large dead

N. fusca trees form parts of the boundary is at Napoleon Hill (Stand 4) where many of the large *N. fusca* trees in the locality have recently died.

The positions of all individuals of *N. truncata* taller than 2 m along a section of the beech forest boundary in a permanent plot are shown in Appendix I.

There does not appear to be a lack of vigour of the *Nothofagus* species, in terms of tree dimensions or regenerative ability near the limits of distribution in the study area.

These observations on boundary patterns apply to unmodified sections of the beech forest boundary along the margins of the main beech forest front, the podocarp-hardwood forest enclaves, the outliers and the main *N. menziesii* boundary within the lowland beech forests.

A comparison of the forest communities on either side of the beech forest boundary at a particular site reveals major differences in stand structure, but not in floristic composition. The beech species dominate the stands they occupy, both numerically and structurally, and occupy a high proportion of the subcanopy at all levels. Beech canopy trees are able to overshadow completely other hardwood species, including *Metrosideros umbellata*, and to reach into the lower foliage layers of the emergent podocarp species. The density and, in some cases, the stature of the other stand components is accordingly greatly reduced. Differences in the densities and population structures of the important podocarp and hardwood species in both beech-podocarp and podocarp-hardwood communities are described in section 4.10.

4.5 DISPERSION AND SPECIES COMPOSITION OF OUTLIERS

A total of 295 outliers were located within the study area, but as small outliers were often difficult to find, this number is likely to be an underestimate. A number of outliers have probably been destroyed by human activity.

The locations, species composition and sizes of all outliers are depicted in Figs 8, 9. 10, 11 and 12.

The outliers can be divided into two groups on the basis of species composition and location:

(i) Outliers in the southern Paparoa Range above 370 m a.s.l.; these are all composed of *N. menziesii* and are referred to as 'upland outliers'.

(ii) Outliers below 370 m a.s.l. on the lower slopes of the Paparoa Range and elsewhere throughout the study area; all four *Nothofagus* species are present in this group of outliers which are referred to as 'lowland outliers'.

Of the total of 295 outliers, 127 are in the lowland category and 168 in the upland category.

In the following analysis, the occurrence of more than one species in an outlier beyond the main beech forest area is treated as a single outlier and not as multiple outliers.

The 'lowland' outliers occupy all types of growing sites (Table 8) but show a preference for relatively open sites and unstable sites with recent soils subject to ground disturbance or siltation. A higher proportion of the outliers appear to occupy gullies, intermediate and high outwash terraces and river flats than would be expected from the occurrence of these growing sites in the landscape. Steep-sided gullies cover only a very small proportion of the total area, yet 15% of outliers are located wholly or partially in gullies. Of the seventeen outliers on high or intermediate terraces, five are confined to the well-lit terrace edges and many of the remainder occur within or adjacent to low open-canopied forest dominated by *Dacrydium colensoi, D. biforme, Leptospermum scoparium* and *Phyllocladus alpinus*. The evidence presented in Table 8 also suggests that outliers are not confined to a single site type but can spread on to adjoining sites.

Table 8: Site preferences of lowland outliers

Growing site[1]	No. of outliers occupying one site type only	No. of sites occupied by part of an outlier
Ridge crests	5	2
Slopes	38	8
Talus fan	2	0
Gully	7	12
Intermediate & high outwash terraces	17	8
Low outwash terraces	7	1
Moraines	2	0
River flats	35	4
	113	

[1] from Bowen (1964), Gregg (1964), Warren (1967) and Mew (1980).

Of the 127 lowland outliers, most comprised a single species (predominantly *N. fusca*). An appreciable proportion contained a mixture of species (Table 9). *N. fusca* was present in all of the mixed species outliers.

Table 9: Species composition of lowland outliers

Number of single species outliers:				Total No.
N. fusca	*N. truncata*	*N. solandri* var. *cliffortioides*	*N. menziesii*	
59	4	2	13	77
Mixed species outliers:[1]				
2 species	3 species	4 species		
24	6	1		31
Not positively identified (outlier not visited)[2]				19

[1] *N. menziesii* outliers within the main area of beech forest (cf. Fig 14) are included in the single species category.

[2] Binocular viewing indicated *N. fusca* in most of this group.

Fourteen of the 31 mixed species outliers for which species identifications were made contained hybrid individuals; seven of these contained adult trees of one species and hybrid individuals, but lacked adults of the other presumed parent species. One outlier was a single individual with hybrid characteristics intermediate between *N. fusca* and *N. solandri*.

In contrast with the lowland outliers, all of the 168 upland outliers consisted solely of *N. menziesii*.

The outliers range in size from very small stands comprising single individuals (seedlings or adults) to stands of up to 360 ha in area. Most are small; 44% are single individuals and 70% are less than 0.2 ha in area. Most of the total area occupied by the outliers is contributed by the largest four, which together cover 1105 ha of the total area of 1330 ha. The frequency distribution of outlier size (Fig 15) demonstrates the predominance of smaller stands and the presence of more stands larger than 2 ha than would be expected on the basis of a linear decline in the frequency distribution.

Small lowland outliers (less than 0.2 ha) predominantly contain one species (Fig 16). As lowland outlier size increases the number of species present also tends to increase.

Most outliers are close to the potential parent stand; 57% are within 200 m of the parent stand (Fig 17). The most distant outlier, at Blackwater Creek (Fig 11), contains *Nothofagus menziesii* which is 15.6 km distant from the nearest potential parent parent stands near the lower reaches of the Arnold River The frequency of outliers declines exponentially with increasing distance from the parent stand, but beyond 5000 m there is a small number of stands more distant than expected from the predominantly linear relationship of the frequency distribution (Fig 17). Of the eleven stands in this category, seven are found in a group to the east of Lake Brunner. Another is the large Blackwater Creek outlier.

Most single-species lowland outliers are found close to the boundary of the potential parent stand, whereas multiple-species outliers are more often located at some distance from the nearest potential parent stand (Fig 18). Some multiple-species outliers however, are close to a potential stand and some single-species

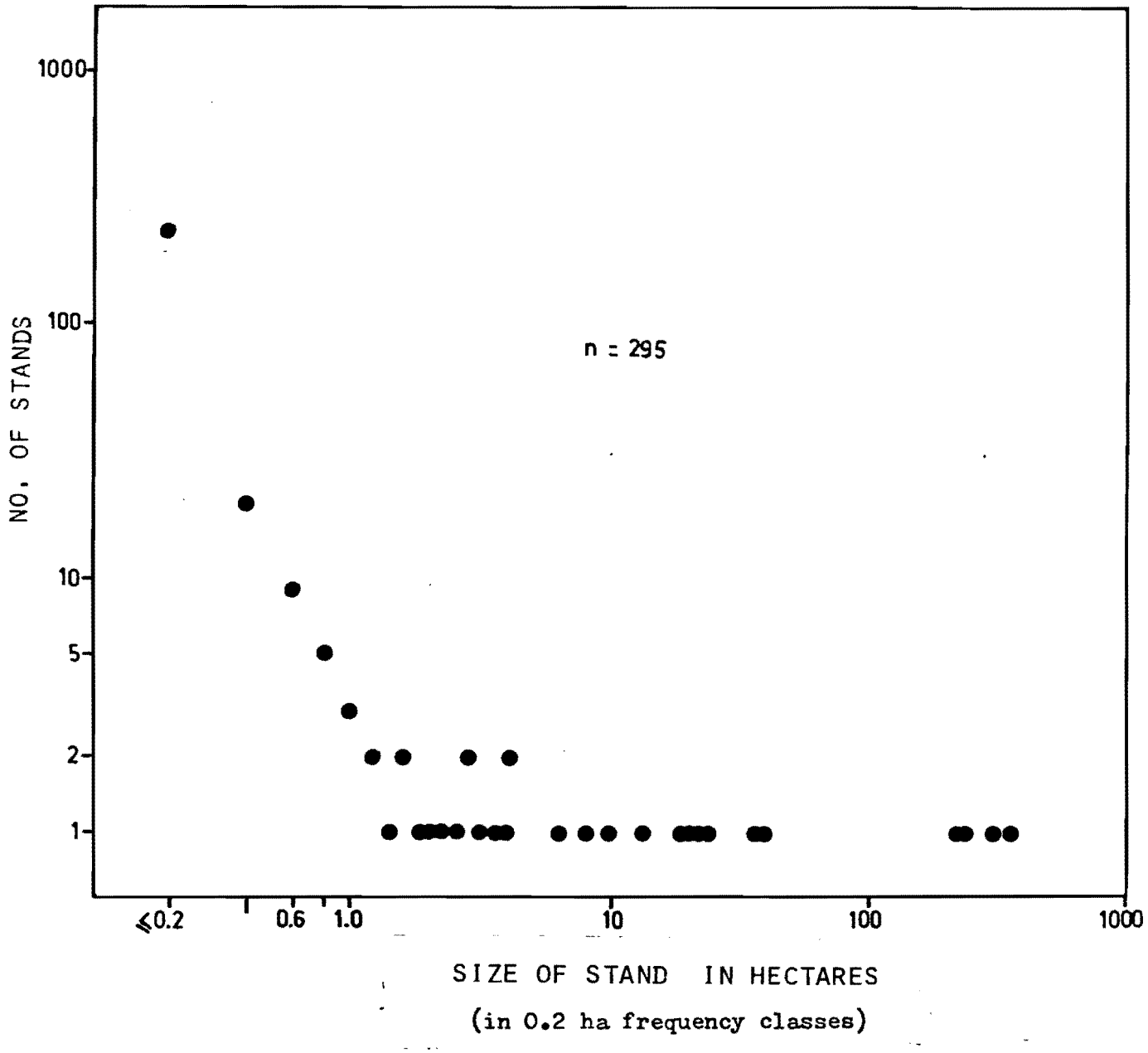
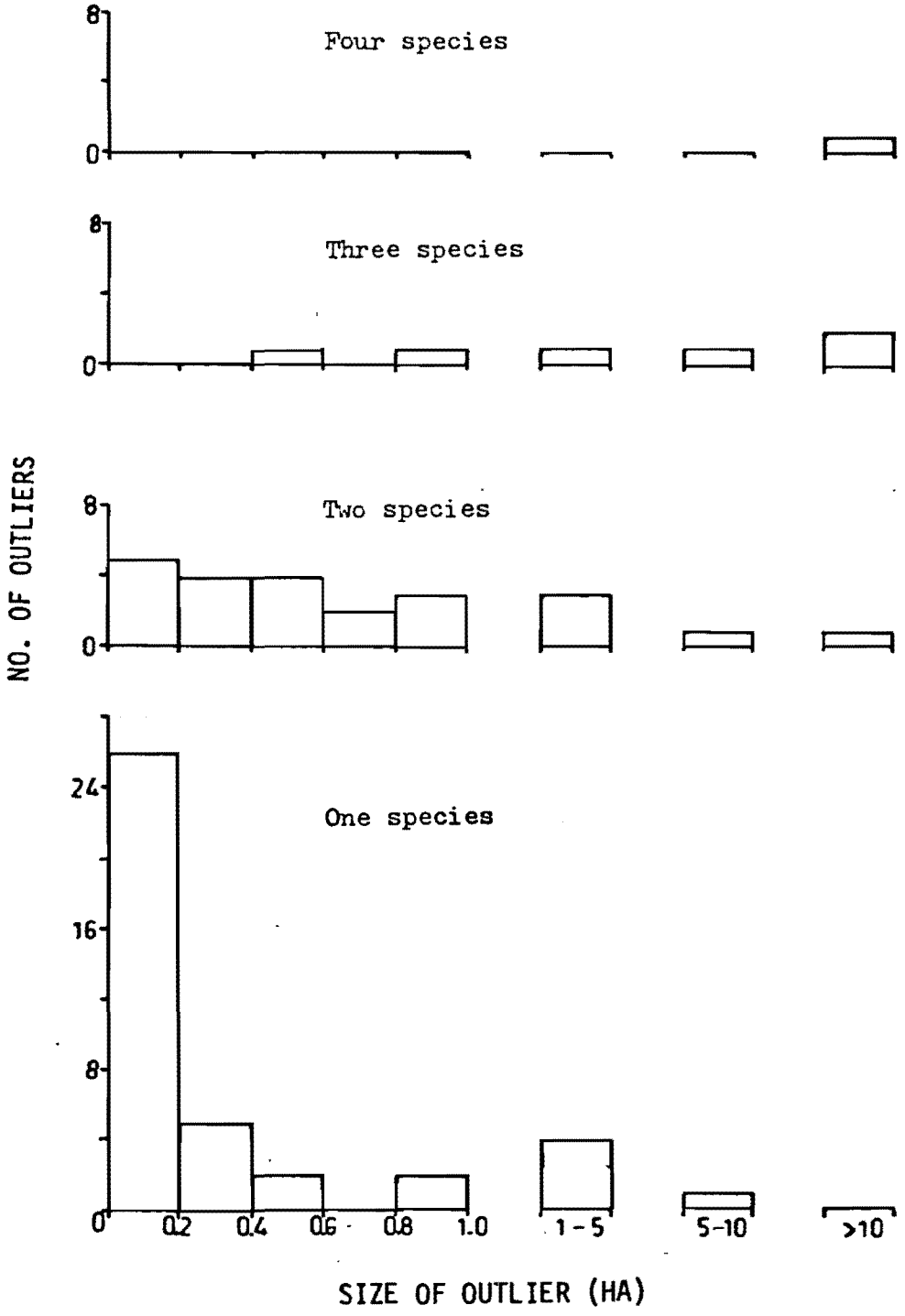


Figure 15 Size-frequency distribution of beech forest outliers in the North Westland study area.

Figure 16: The species composition of lowland outliers of different size (single individuals are not included).



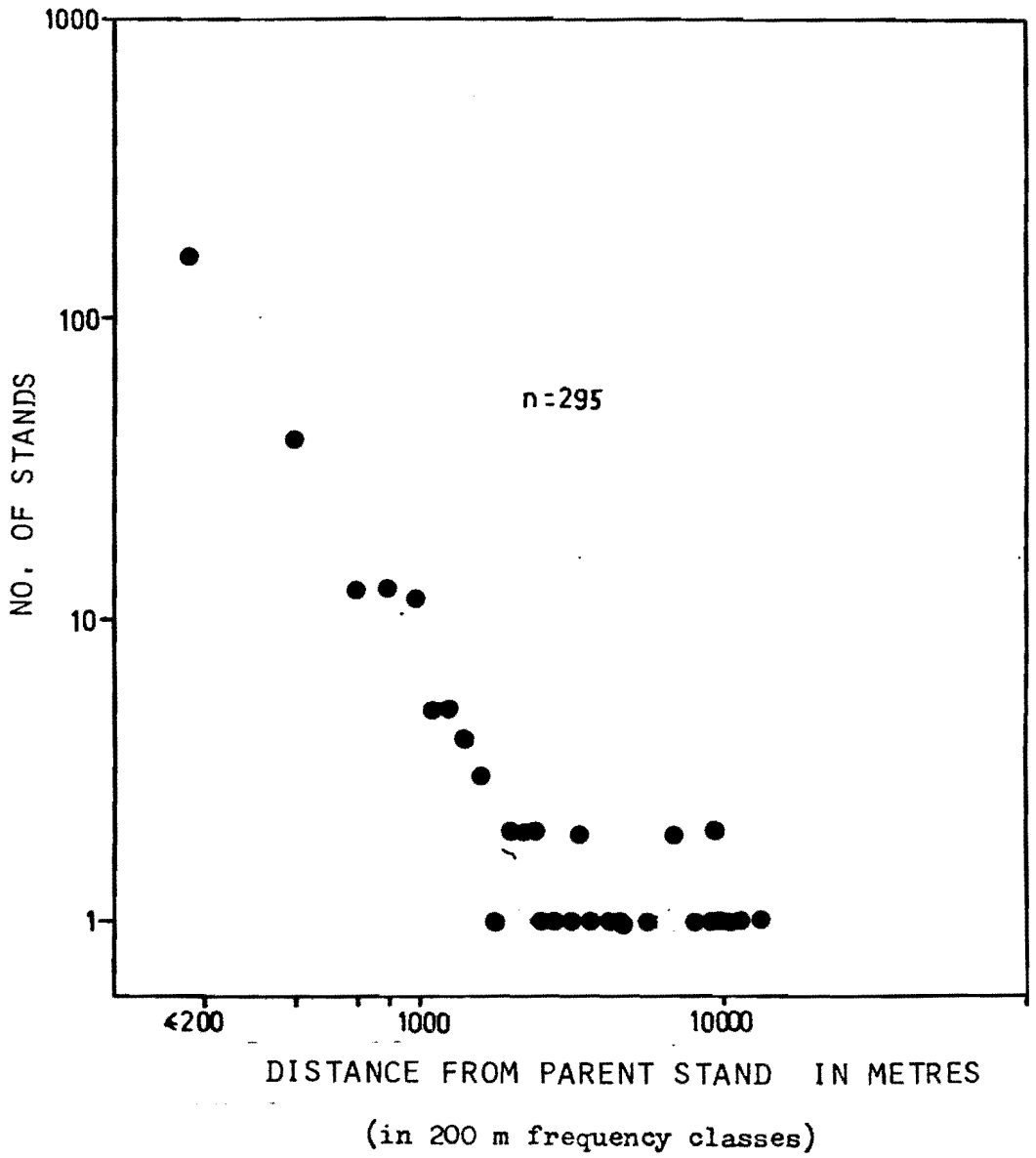


Figure 17: Distances of beech forest outliers from potential parent stands.

Figure 18. The species composition of lowland outliers at different distances from the potential parent stand.

Only outliers where species identifications were made are included in this analysis. Nothofagus menziesii outliers within beech forest are not included.

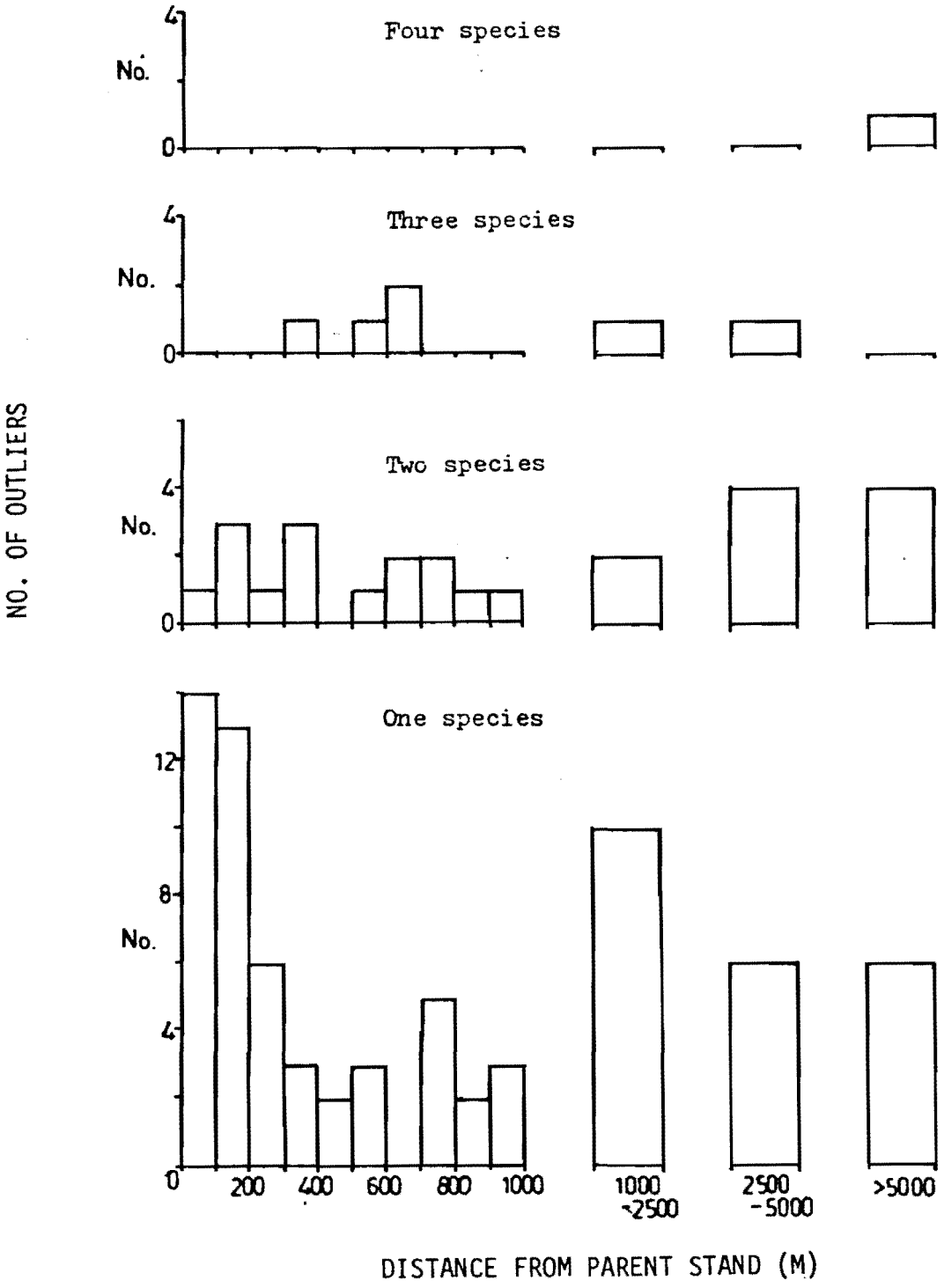


Table 10: Frequencies, total areas and perimeters of outliers

	Upland outliers	Lowland outliers
Area available[1]	36 km^2	825 km^2
Frequency of outliers	4.7/km^2	0.15/km^2
Area of outliers	520 ha	810 ha
Length main boundary	38 km	297 km
Length outlier boundaries	45.5 km	75 km

[1] excluding water surfaces and the area above the *N. menziesii* timberline.

outliers are very distant. The predominance of single-species outliers near the potential parent stand may be a function of outlier size in light of the tendency of the smaller outliers to be located close to the parent stand boundary (see Fig 19), and of smaller outliers to contain one species (Fig 16). Thus the number of species in an outlier appears to be related more to the size of the outlier than the distance from the nearest larger area of beech forest containing the species found in the outlier.

The relationship between outlier size and distance from potential parent stands for both lowland and upland outliers is shown in Figure 19. Nearly 80% of the outliers are both small (< 1 hectare in area) and close (<1 km) to the parent stand. There is a group of predominantly lowland outliers which are both small and distant from parent stands. The most distant of this group (beyond 6 km from parent stands) are all located in the Moana - Bell Hill district. The large upland outliers, situated in the headwaters of Roaring Meg and Moonlight Creeks, are relatively close to the presumed parent stands across the tussock grasslands of the crest of the Paparoa Range. In contrast, the two largest lowland outliers at Deep Creek and Blackwater Creek are found at some distance from potential parent stands. These two stands are well separated from other outliers in the figure 19 plot. Three other lowland outliers tend to form a separate grouping; being moderately large (between 8 and 20 hectares) and between 3 and 7 km from potential parent stands. These three outliers are found at the Orangipuku River, Red Jacks Creek and near Lady Lake.

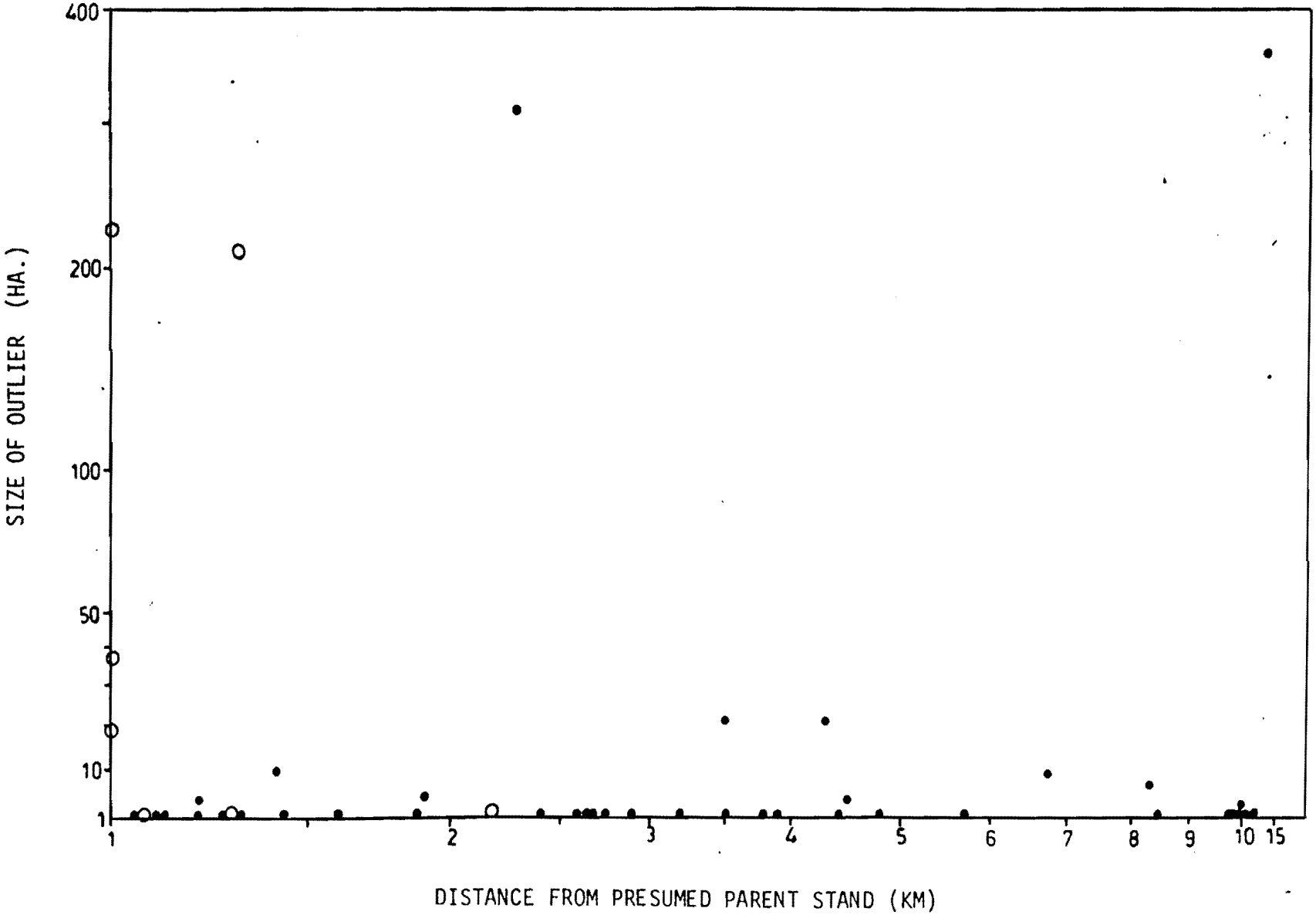
The frequencies of outliers in an area within 15 km of the main beech forest boundary (the range within which all outliers are located) are shown in Table 10 together with estimates of the area of outliers and their total boundary perimeters in relation to the length of the main boundary.

The frequencies of single- and multiple-species lowland outliers are shown in Table 11, together with expected frequencies based on the frequency of single-species outliers and taking multiple-species outliers to be the consequence of two, three and four independent dispersal events. The probability of joint occurrences of independent events is the product of the individual

Figure 19. The relationship between outlier size and distance from potential parent stand.

(Outliers < 1 hectare in size and/or <1 km from the potential parent stand are excluded.

A further group of outliers < 5 hectares and < 1 km from parent stands is not shown. Open circles are upland outliers and closed circles lowland outliers).


400
200
100
50
10
1
SIZE OF OUTLIER (HA.)
1
2
3
4
5
6
7
8
9
10
15
DISTANCE FROM PRESUMED PARENT STAND (KM)

probabilities. Thus the actual frequency of single-species lowland outliers is 0.0824 km^2, the expected frequency of two-species outliers is 0.0824^2 = 0.00679/km^2, the expected frequency of three-species outliers is 0.0824^3 = 0.00056/km^2 and the expected frequency of four-species outliers is 0.0824^4 = 0.000046/km^2. For a comparison with actual numbers of outliers, these expected frequencies are converted to expected numbers of outliers (Table 11).

Table 11: Observed and expected frequencies of multiple-species lowland outliers

Number of species	Number of outliers[1]	Expected number of outliers
1	68	-
2	24	5.6
3	6	0.46
4	1	0.038

[1] Unidentified outliers (n = 19) and outliers of *N. menziesii* within the main beech forest (n = 9) not included.

The observed frequencies of two-, three- and four-species outliers are significantly greater ($P<<0.01$) than would be expected on the basis of each species arriving independently in the outlier (Table 11). Differences in the frequencies were tested using a method based on the arcsine transformation (Sokal & Rohlf, 1969, p 607).

4.6 ESTABLISHMENT OF *NOTHOFAGUS* IN COMMUNITIES LACKING *NOTHOFAGUS*

4.6.1 Experimental sowing

Seedlings derived from seed experimentally sown in podocarp-hardwood forest away from *Nothofagus* trees all appeared unhealthy at the time of sampling at the beginning of their third growing season. The seedlings had unusually small leaves and lacked the normal green pigmentation of seedlings from *Nothofagus* forest. There was little height increment since the initial season's growth. No seedling had grown more than 0.5 cm in height, in comparison with seedlings from *Nothofagus* forest which showed height increments of up to 8 cm in their second growing season. Mycorrhizal sheaths were present on the short roots of some seedlings although the degree of infection was not as high as seedlings of comparable age collected from *Nothofagus* forest. Both *N. truncata* and *N. menziesii* seedlings had mycorrhizal sheaths in their third growing season, but *N. fusca* and *N.solandri* var. *cliffortioides* seedlings did not. Seedlings of all four species from *Nothofagus* forest had abundant mycorrhizal infections.

4.6.2 Mycorrhizae in isolated *Nothofagus* stands

Mycorrhizae were present in the roots of *N. truncata*, *N. fusca* and *N. solandri* var. *cliffortioides* in each of the six outlier stands examined, and in other outliers in which a field inspection for mycorrhizae was made.

4.6.3 Naturally established seedlings

A number of seedlings and saplings of *N. fusca* and *N. menziesii* were found as outliers beyond the boundaries of existing beech stands (see sections 4.2 and 4.5). The *N. menziesii* seedlings (totalling 68 seedlings chiefly in two groups) were all established in tussock grassland near the crest of the Paparoa Range, except for one sapling in beech-podocarp forest near the banks of Hatters Creek in Granville State Forest (Fig 10). Two *N. fusca* seedlings were located beyond beech forest boundaries: one in undisturbed podocarp-hardwood forest at Nelson Creek (Fig 10) and one in manuka scrubland at a pakihi margin at the head of Callaghans Creek (Fig 10). All of these seedlings and saplings were healthy, taller than 50 cm and appeared to be successfully established.

In addition, two groups of *N. fusca* seedlings were found along the abandoned, gravelled forestry roads on Lake Hill Ridge (S45/148842, 117847, Fig 10). The furthest seedlings were 250 m from the nearest beech trees. These examples show how grossly disturbed sites with newly-exposed surfaces can be more readily colonised by beech seedlings growing beyond the previous range of beech forest than undisturbed sites. It is possible that the colonisation of tussock grassland in the Paparoa Range by *N. menziesii* just described followed a deliberately lit fire. The manuka scrubland near Callaghans Creek colonised by one *N. fusca* seedling was induced by human disturbance, presumably fire.

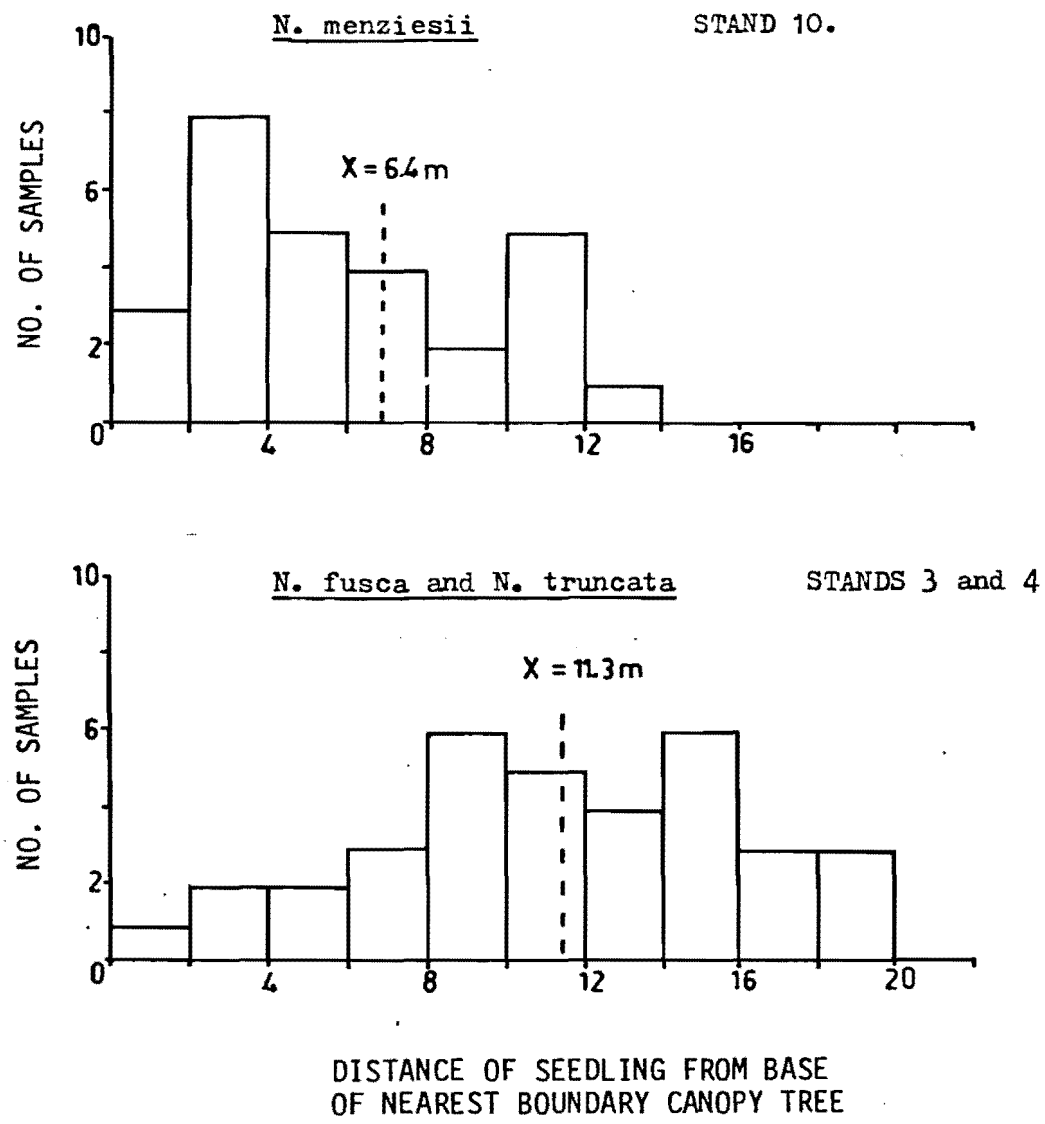
4.6.4 Seedling establishment on the margins of existing stands

Nothofagus seedlings are found along the margins of existing stands beyond the canopy limits of boundary trees. Where intact podocarp-hardwood forest borders the *Nothofagus* stand, seedlings are uncommon or absent under the canopy of the podocarp or hardwood trees, but are almost invariably present in canopy gaps where they show signs of active growth and where all stages of seedling development leading to recruitment to the canopy can be observed.

Where subalpine scrubland or tussock grassland adjoins the margins of beech forest, seedling establishment is not dependent on the formation of openings through the death of dominants in the invaded vegetation. Seedling establishment in these cases proceeds all along the stand margins.

N. menziesii seedlings in Stand 10 (in a sample taken in conjunction with the estimation of rates of marginal spread, section 4.7) established at a mean distance of 6.4 m from the trunk of the boundary tree, with the most distant seedling being 13.3 m from the boundary tree (Fig 20). The canopy of the boundary trees where these measurements were made extended for up to 4.4 m in horizontal projection, with a mean range of 3.0 m. A large proportion of the seedlings, therefore, have established near the canopy margins of the boundary trees. *N. fusca* and *N. truncata* seedlings at Stands 3 and 4 have established at a mean distance of 11.3 m from the trunk of the boundary tree (mean for *N. fusca* = 11.0 m, for *N. truncata* = 11.7 m) with the most distant seedling being 18.6 m from the parent tree (Fig 20). The canopy of the

Figure 20. The range of seedling establishment along Nothofagus forest margins.



boundary trees where the measurements were made extended for up to 7.6 m in horizontal projection with a mean range of 3.8 m. Most *N. fusca* and *N. truncata* seedlings, therefore, have established well beyond the canopy margins of the boundary trees.

The range of seedling establishment distances described above was confirmed by other observations made along undisturbed sections of the boundaries. *Nothofagus* seedlings are frequently found beyond the canopy limits of boundary trees, but are rare more than 20 m from the trunks of the boundary trees.

4.7 RATES OF *NOTHOFAGUS* MIGRATION

Rates of marginal spread

A total of 41 pairs of individuals were measured at the beech forest boundary to obtain estimates of the rate of marginal spread. The resulting age and inter-tree distance data are summarized in Table 12, together with the mean rates of marginal spread derived from them them. The differences between sample locations for the *Nothofagus truncata* and *N. fusca* estimates were found to be not significant (pairwise comparisons using Student's t-test, $p>0.05$), hence the data are presented by species.

The differences in rate of spread estimates and inter-tree distances between the three species (Table 12) are not significant (pairwise comparison using Student's t-test, $p>0.05$), despite the distinctly different sites sampled where the vegetation being invaded by the *Nothofagus* species ranged from low, open scrubland to tall, closed-canopy podocarp-hardwood forest. It should be noted that these estimates apply to the past 350 years, the maximum age among the trees sampled.

Table 12: Estimates of rates of marginal spread (means with standard deviations).

Species	Age a (yrs)	d_1 (m)	Age b (yrs)	d_2 (m)	Age c (yrs)	Migration rate (m/yr)
N. menziesii	185 (n = 2)	9.2 (n = 2)	145±58.2 (n = 7)	10.4±2.0 (n = 5)	21±16.5 (n = 5)	0.09±0.02 (n = 7)
N. truncata	247±74.5 (n = 6)	13.8±5.8 (n = 6)	146±77.0 (n = 16)	12.4±4.0 (n = 12)	22±15.2 (n = 12)	0.11±0.06 (n = 18)
N. fusca	260±69.6 (n = 6)	14.0±3.3 (n = 6)	151±91.9 (n = 15)	13.4±4.1 (n = 10)	17±11.1 (n = 10)	0.12±0.07 (n = 16)

These results demonstrate a slow rate of migration by marginal spread from existing boundaries into stable vegetation. The overall mean rate from Table 12 is 0.11 m/yr or 11m/100 years (95% confidence limits of the mean are 7 to 13m/100 yrs).

The mean rate is higher than the estimate of 6m/100 yrs (0.06 m/yr) derived by a similar method for a sample of 16 estimates for the marginal spread of *N. menziesii* in the Paringa district (Wardle, 1980a). Wardle did not estimate tree ages individually but derived them from a stem size -age relationship based on cores taken from another sample of trees.

Potential migration rate

Given estimates for effective dispersal distances from parent trees and the time taken for an individual to attain a seed bearing age as a canopy tree, a potential rate of migration can be derived. Dispersal distance is assumed as the inter-tree distances d_1 and d_2 in Table 12. Based on the observation that only trees with all or most of their canopy in full sunlight produce viable seed, estimates of the time taken to reach canopy tree status gave minimum seed-bearing age estimates of 60 years for *N. truncata* and *N. fusca* in tall forest. In the case of *N. menziesii* invading low scrubland, the development of a mature crown above the scrub species takes about 60 years also.

Using the estimates for earliest seed-bearing age and mean dispersal distances, and assuming seedling establishment from the first seed falls, the potential migration rates would be 0.17 m/yr for *N. menziesii*, 0.22 m/yr for *N. truncata* and 0.23 m/yr for *N. fusca*. These rates are approximately twice the rates estimated from age profiles (Table 12). The differences between the two sets of estimates (potential and actual) are an indication of the resistance of the existing vegetation to invasion by *Nothofagus* species. The invading species require canopy gaps in full forest for successful establishment and growth to maturity (section 4.6). As canopy gaps in stable vegetation are restricted in extent and duration, the rate at which invasion can proceed is slowed by their limited availability.

Migration rates on other sites

The beech forest boundary protrudes in a number of places, forming 'fingers' of beech forest extending along valleys and across terraces in the Grey Valley and across the upper slopes of the southern Paparoa Range (section 4.2). Assuming that beech

forest is extending its range, these protrusions of the boundary indicate more rapid migration on particular sites, namely the alluvial terraces and the low and intermediate outwash terraces and the upland zone of the mountain ranges. In a few places, for example in the vicinity of Roaches Creek, Mawhera State Forest (Fig 10), protrusions across the central, poorly-drained sections of high outwash terraces indicate that these may also be sites favourable to migration.

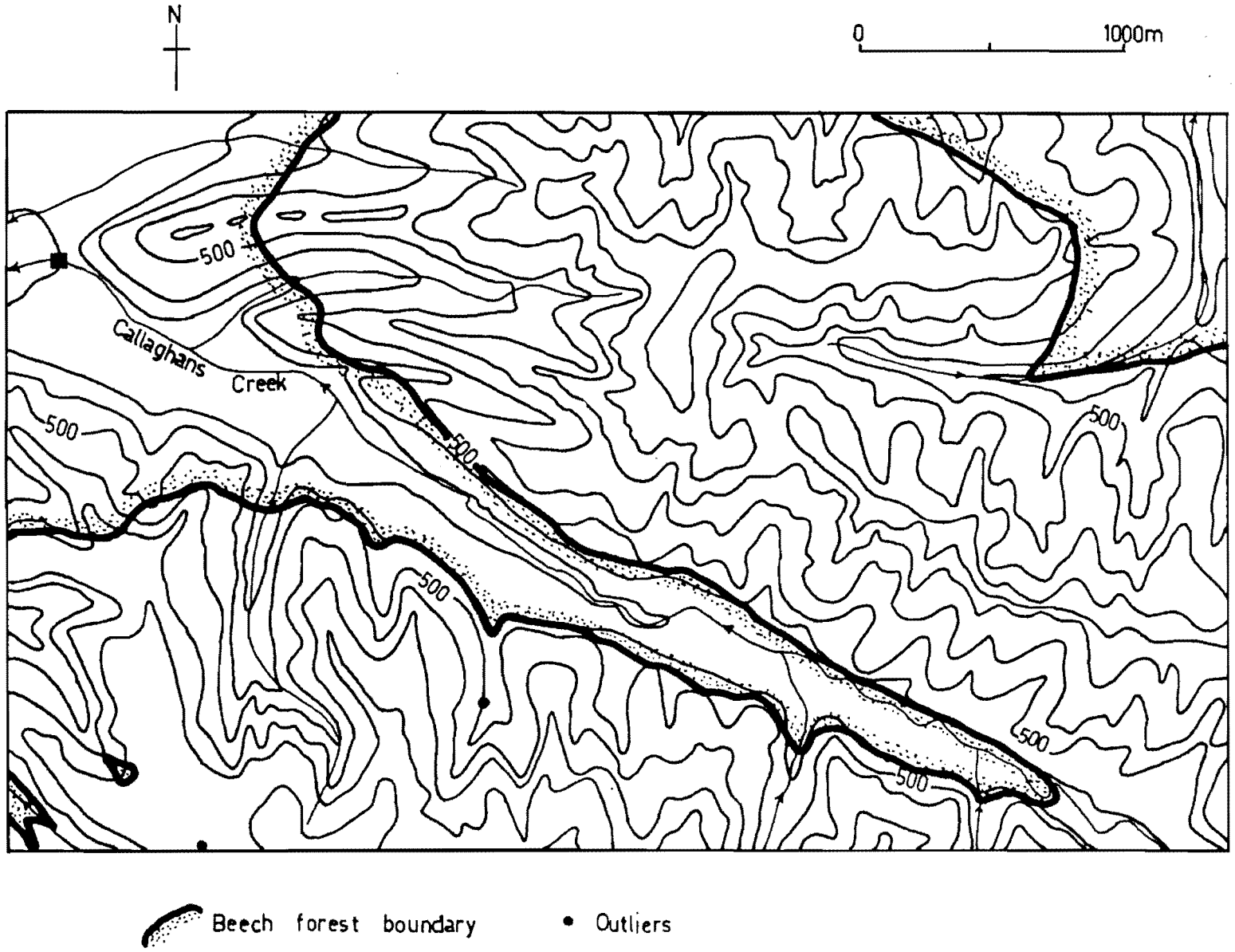
Where beech forest extends into valleys, the boundary is located part-way up the valley sides at the entrance of the valley, and steadily loses altitude towards the valley head until only the stream banks or flood plain are occupied by beech forest. An example is illustrated in Fig 21. This pattern is consistent with migration upstream into the valley, and with a more rapid rate of migration along the valley floor than up the sides of the valley. From a presumed entry point at the valley entrance, the ratio of distances measured across the ground to the highest point reached by the boundary on the slopes and the furthest point reached up the valley floor provides a measure of relative migration rates across different sites.

A number of valleys in the Grey Valley containing beech forest protrusions were examined in this way. The ratios of distance traversed along the valley floor to the distance traversed up the valley sides are as follows:

2.1 in Sunday Creek	(950m along valley floor, 450m along valley sides; Fig 9),.
2.7 in German Gully	(1600m along valley floor, 600m along valley sides; Fig 10),
3.6 in Dead Horse Creek	(1250m along valley floor, 350m along valley sides; Fig 10),
4.1 in Twelve Mile Creek	(7925m along valley floor, 1950m along valley sides; Fig 9),
4.4 in Roaring Meg Creek	(2200m along valley floor, 500m along valley sides: Fig 9),
4.7 in Callaghans Creek	(4500m along valley floor, 950m along valley sides; Fig 21).

The mean ratio for the six valleys examined is 3.6. For other valleys near the beech forest boundary the likely entry point for migrating beech forest was difficult to determine, or there was no

Figure 21 A finger of beech forest extending into a valley and three small outliers, showing the relationship between the position of the beech forest boundary and topography.
(The square in the upper left-hand corner marks the presumed entry point for migration into the valley, see section 4.7 .
Topographical detail is from NZMS 1 S45.
Contours are in hundred feet (30.5 m) intervals.
500' contour = c. 150 m a.s.l.)


N
0
1000m
500
Callaghans
Creek
500
500
500
500
500
500
Beech forest boundary
Outliers

protrusion of beech forest into the valley.

Several examples of protrusions extending down valleys could be analysed in a similar manner. On the north bank of the Taramakau River, beech forest extends a maximum of 1.8 km upslope and 17.7 km downstream, giving a relative distance ratio of 9.8, see Figs 11 and 12. If the origin of the Deep Creek outlier (section 4.2.8) is assumed to be at the widest, eastern end of the outlier, then the boundary has traversed up to 1.0 km across the terraces adjoining the watercourse and 14.8 km downstream along the alluvial plain of Deep Creek. This gives a relative distance ratio of 14.8. These examples illustrate the comparatively rapid rates of migration possible in a downstream direction alongside watercourses compared with migration in an upstream direction or across land.

A further example of relative migration rates can be derived from the Blackwater Creek outlier (section 4.2.10). If the point of origin for the outlier is taken as its present geographical centre, then the boundary has extended at least 1.5 times further along the adjoining valleys (both upstream and downstream) than across the high terrace. Removal of forest by goldmining has destroyed some of the outlier, and the downstream extension could have been further than indicated by the present boundary.

No examples were found which illustrated the relative migration rates across high terraces compared with hillslopes.

Contribution to migration from outlier establishment

Outlier establishment can lead to a rapid extension of range over relatively long distances. Outliers presumed to have originated from long distance dispersal may be found up to 12 km from presumed parent stands, although most outliers are found within 200 m of the main beech forest boundary, and outliers more than 5 km from a parent stand are rare (section 4.5).

Once established, the outliers expand slowly by marginal spread, only occasionally forming secondary outliers as in the case of the Blackwater Creek outlier (Fig 11). A total of 295 outliers are located within 15 km of the main boundary (the distance within which all outliers are located), which represents a density of 0.15 outliers/km^2 in the lowland forests and 4.7 outliers/km^2 in the upland zone of the southern Paparoa Range. The low density

of outliers in the lowland zone, and the small proportion of the available area occupied, 810 hectares in a total of 82 500 hectares (Table 10), indicates that the contribution of outliers to the expansion of range is a small one in this area. The main lowland boundary (297 km) is much longer than the total boundaries of the outliers (75 km). These figures indicate that if marginal spread occurs equally along all boundaries, the outliers potentially contribute 20% of the expansion of the *Nothofagus* range by this method.

In the upland zone of the southern Paparoa Range the situation is different. Here the outliers are more frequent and cover a significant proportion of the area outside the main beech forest boundary (520 hectares in a total area of 3600 hectares; Table 10). The total boundaries of the outliers (45.5 km) are longer than the main boundary (38 km) and outliers potentially contribute 54% to the expansion of range by marginal spread.

Boundary protrusions in the upland zone of the southern Paparoa Range indicate a more rapid migration in upland sites than in mid-slope sites. Since the rate of marginal spread in upland sites is as slow as marginal spread in lowland sites (Table 12), this rapid migration is most probably due to the more frequent formation of outliers.

Estimates from the historical and fossil records

There are three dated appearances of *Nothofagus* in the postglacial fossil record in the north Westland region (Moar, 1971) which were used to derive estimates of the postglacial migration rate. These are in the upper Maruia valley where *Nothofagus* was estimated to have spread at about 6500 years B.P., in the Upper Grey valley where *Nothofagus* enters the record at about 6000 years B.P., and in the Bell Hill area where the spread of *Nothofagus* in the vicinity began at about 2400 years B.P. These localities are shown on Fig 26. Migration rate estimates were derived from this information and the estimated distances along valleys between the sites assuming a north to south migration pattern with no other sources (Table 13). In addition, minimum migration rates were estimated by assuming migration from two of

the sites to the heads of adjoining montane valleys, the upper Maruia valley to the Lewis Pass and the Lake Christabel catchment. In each case the migration route largely follows watercourses in the floors of wide valleys in both upstream and downstream directions.

Table 13: Migration rate estimates from the fossil record.

Sites	Migration distance (km)	Time interval (yrs)	Migration rate [2] (m/yr)
Upper Maruia[1] - Upper Grey[1]	16.8	c. 500	33.6
Upper Grey - Bell Hill[1]	48.0	c. 3600	13.3
Upper Maruia - Lewis Pass	24.2	< 6500	> 3.7
Upper Grey - Lake Christabel catchment	18.5	< 6000	> 3.8

[1] From Moar (1971).

[2] These estimates are not significantly altered using corrected ^{14}C dates Appendix III

There are major uncertainties in these estimates. Each date for *Nothofagus* arrival has an error associated with radiocarbon dating and an unknown uncertainty associated with interpolation in the peat profile. There is also uncertainty about migration routes; for each pair of sites alternative sources of expansion are possible, for example, from the east of the Main Divide in the case of Lewis Pass and to the north of Lake Ahaura in the case of Bell Hill. These alternative sources would mean that migration rates are much lower than estimated, which may explain why the two fastest estimates derived from the fossil record (33.6 m/yr and 13.3 m/yr) are up to 300 times more rapid than across-ground estimates from age profiles (Table 12) and up to 20 times the rates derived for other, more favourable migration sites in the Grey Valley. The two slower estimates (>3.7 m/yr and >3.8 m/yr), however, are within the same order of magnitude as

derived estimates of downstream migration in valleys, although these estimates also are higher than estimates for different sites in the Grey Valley. Because of the uncertainties associated with obtaining migration rate estimates from an inadequate fossil record, more definite conclusions cannot be made. It is possible that migration in the glaciated montane valleys of north Westland was more rapid than elsewhere (see section 5.5.4).

No suitable historical records were found which could be used to estimate migration rates. The period covered by aerial photography (the last 35 years) is too short in relation to the slow rates of migration to be useful. Photographs taken from the same position on the ground over a longer period have potential value for quantitative estimates. An example is given by Kirkland (1973) which shows a very slow rate of recolonisation of cleared land over a 100 year period at Globe Hill near Reefton.

4.8 THE POSITION OF THE BEECH FOREST BOUNDARY

The present position of the beech forest boundary in north Westland can be examined in relation to climatic, floristic, soil and topography-related site variation on both local and regional levels.

The position of the boundary does not generally conform with topographic or other site features. In many places the boundary crosses landform or soil boundaries, and favourable sites adjoining the boundary are often not occupied by beech forest. There is, however, a tendency for the boundary to be located on valley floors and adjoining lower slopes or on ridge crests in some areas (Figs 8, 9, 10, 11 and 12).

The varying relationship between the position of the boundary and site is illustrated in Figure 21 which shows a section of the beech forest boundary in the Grey Valley taken from Fig 10. Beech forest comprising *N. fusca* and *N. truncata* extends along the valley of Callaghans Creek where it occupies stream bank and alluvial terrace sites. Towards the entrance of the valley, beech forest extends upslope from the valley bottom and the boundary steadily rises in altitude, crossing upper slopes, gullies and ridge crests at oblique angles. This example illustrates the general tendency for the boundary to be located in valleys and also the wide range of growing sites covered by the boundary. Further examples are shown in Figures 8 to 12.

It is unlikely that the nature of the soils limits the spread of *Nothofagus* species beyond their present limits as the same broad soil groups occur within the beech forest area of north Westland and in central Westland (Gibbs *et al.*, 1950; N.Z. Soil Bureau, 1968; Mew & Leamy, 1977; Mew, 1980). The *Nothofagus* species are capable of occupying the full range of forest soils found in north Westland with the exception of minor areas of coastal, limestone and poorly-drained terrace soils.

There is an overall decline in lowland plant species diversity from north to south Westland as the southern limits of species are successively reached. The southern limits of some lowland species fall within the same general area but do not coincide with the limits of *Nothofagus* distribution in north

westland. Higher plant species with inland southern limits within 30 km to the north and south of the main beech forest front are (with location of limits in brackets): *Metrosideros parkinsonii* (Mount Te Kinga), *Senecio hectori* (Runanga), *Coprosma robusta* (Kumara), *Tetraria capillaris* (Goldsborough), *Gahnia pauciflora* (Otira), and *Senecio rufiglandulosus* (Aikens) (C.J. Burrows, pers. comm.; Wardle, 1980c; personal observations). Within the same latitudinal range ten higher plant species reach southern limits in coastal or near coastal locations. Included in this group are *Dodonaea viscosa, Brachyglottis repanda* and *Epacris pauciflora*. Some of these species at their southern limits inhabit rocky bluffs or limestone ridges. These habitats are only intermittently present for a long distance along the coastline south of Greymouth.

Altogether, about 70 lowland species of higher plants reach southern limits for the western South Island at various places throughout Westland. None of these species limits coincides with those of *Nothofagus* in north Westland, but a grouping of six species with inland limits and ten species with coastal limits have southern limits of distribution which fall within 30 km to the north and south of the main *Nothofagus* front (previous paragraph). It is difficult to ascertain whether these groupings of lowland species limits indicate a floristic boundary correlated with the limits of *Nothofagus* distribution in that region. For some species, in particular those with coastal limits, the limits of distribution may be determined more by the availability of favourable habitats with special soil conditions or freedom from frosts than by a regional climatic pattern.

One alpine species, *Chionochloa australis* has southern limits similar to those of *Nothofagus* in north Westland, and another seven alpine species centred on Nelson and Marlborough reach southern limits in the Taramakau to Waimakiriri area close to the *Nothofagus* limits on the western side of the Southern Alps (C.J. Burrows, pers. comm.). It is possible that these coincident species limits reflect a climatically-related regional floristic boundary in north Westland, although the availability of suitable habitats and the history of the vegetation may also influence the distribution patterns. The southern limits of some species could

represent migration from glacial period refugia proposed for the north-west of the South Island (Wardle, 1963a; Burrows, 1965).

The overall distribution of beech forest in Westland does not conform with the known regional patterns of climatic variation described by Garnier (1958) and Coulter (1973). *Nothofagus* is found at all positions on the gradients of major climatic elements such as rainfall and mean temperature (where forest is present). Thus beech forest occupies both the wettest areas of the region in the south and the driest areas, in the central Grey Valley and near Westport. Beech forest is also found along the topography-related temperature gradient of increasing mean temperature from timberline to the coastline.

With the exception of rainfall measurements the lack of climatological data prevents a detailed examination of the relationship between the distribution of *Nothofagus* and the climate in north Westland. The distribution of annual rainfall does not conform with the southern limits of *Nothofagus* (Fig 22).

A high incidence of fog and cloud has been linked with the absence of *Nothofagus* from some areas of the Tararua and Ruahine Ranges (Zotov *et al.*, 1938; Elder, 1965) and with the absence of *N. menziesii* in central Westland (Zotov, 1938). Although adequate records of fog and cloud cover are not available to test this hypothesis for Westland, the presence of *N. menziesii* in areas with a high incidence of fog and cloud, such as the upper seaward slopes of the Paparoa Range, suggests that this factor is not limiting the distribution of this species in central Westland. Wardle (1964) has suggested that high rainfall or frequent fogs would slow but not prevent *Nothofagus* invasion.

Figure 22. The beech forest boundary in north Westland in relation to annual rainfall.

KEY

Annual rainfall isohyets (mm) (1941-1970 records, N.Z. Meteorological Service, Wellington)

Hatched area - annual rainfall greater than 5600 mm.

Beech forest boundary.

Main Divide.

Recording stations.

In mountainous areas where there are very few stations and often large rainfall gradients, the isohyets only indicate the general pattern of rainfall distribution. In such areas they cannot be used to obtain an accurate estimate of rainfall.


Buller R.
4000
3200
2800
4000
4800
2000
2800
3200
Grey R.
3200
2000
2000
2400
2000
1600
2000
2400
Maruia R.
Lewis Pass
GREYMOUTH
4800
4800
1600
2800
3200
4000
4800
Arthurs Pass
2000
0
10 km

4.9 MIGRATION ROUTES

Nearly all forested sites in north Westland are available as migration routes for the *Nothofagus* species. The exceptions are limited to some coastal and swampy sites. As well as the forests, some parts of the subalpine scrub and alpine grassland vegetation can be invaded.

On the basis of evidence from the orientation of the present beech forest boundary, migration takes place preferentially along certain routes (section 4.7). These routes primarily follow the floors of the more open valleys, particularly those with an alluvial flood plain. These valleys provide a migration route in both upstream and downstream directions. Examples of apparent upstream migration include the Arnold River, Twelve Mile Creek, Callaghans Creek and Red Jacks Creek. Downstream migration is evident in the Taramakau and Grey Rivers, Deep Creek, Blackwater Creek and Roaring Meg Creek (Figs 6, 9, 10 and 11). Some valleys close to the main beech forest boundary lack a protrusion of beech forest. These narrow valleys with watercourses confined by steep, high banks do not provide a favourable migration route. Examples include Sunday Creek (Mawhera State Forest), Blackwater Creek (Brunner State Forest) and other small streams (Figs 9 and 10). Poorly-drained sections of the intermediate and high outwash terraces also appear to function as preferential migration routes, as for example, on the terraces adjoining the Arnold River, Stillwater Creek and Roaches Creek (Figs 9 and 10). In the southern Paparoa Range the upland zone functions as a primary migration route for *Nothofagus menziesii* with later spread down ridge crests and valley floors (Figs 8 and 9). The more rapid migration on the sites described above means that the slowest migration has occurred on hill slopes in low altitude hill country.

Topographical barriers to migration such as lakes and mountain tops are limited in extent and effectiveness. Rivers can provide a barrier when the direction of the watercourse lies across the direction of migration. A notable example occurs in the Haupiri Valley (Fig 6) where a large area of beech forest on the north bank does not extend across to the south bank until the lower section of the valley is reached. Smaller scale examples can be seen along sections of the Arnold River (Fig 9).

Barriers are provided in some areas by fertile and infertile swamps and by limestone ridges and plateaux in the Punakaiki region.

These barriers can be readily breached in at least some instances by long-distance dispersal. The distribution patterns of beech forest on both sides of the tussock grassland covered tops of the southern Paparoa Range illustrate how readily barriers to migration can be breached.

Directions of migration

The direction of past migration in the immediate vicinity of the present boundary can be inferred from the orientation of the boundary in relation to the local topography and distribution of growing sites. There are four types of situations where migration directions can be derived:

(i) The extensions of beech forest into valleys and on to terraces, with a progressively narrower distribution further away from the main area of distribution indicating the direction of migration.

(ii) Where a ridge or an area of elevated hill country is reached by beech forest, the position at which the high ground is first surmounted shows the direction from which beech forest approached. An example, Lake Hill Ridge to the south of Lake Hochstetter, is illustrated in Fig 23. Here, an isolated ridge occupied by podocarp-hardwood forest is surrounded by beech forest which also extends upslope on the south-eastern flanks, thus indicating a direction of immigration from the south-east. Further examples can be found on nearby Granite Ridge and on ridges immediately to the north of Lake Hochstetter (Figs 11 and 12).

(iii) Where small enclaves of podocarp-hardwood forest occur amidst an extensive area of beech forest occupying a particular range of sites, the position of the enclaves in in relation to the surrounding area can indicate the direction or directions of migration into that area. The isolated block of dissected hill country to the east of Totara Flat (Granville State Forest) contains two groups of podocarp-hardwood forest enclaves (Fig 10). The position the enclaves in the south-western corner and near the centre

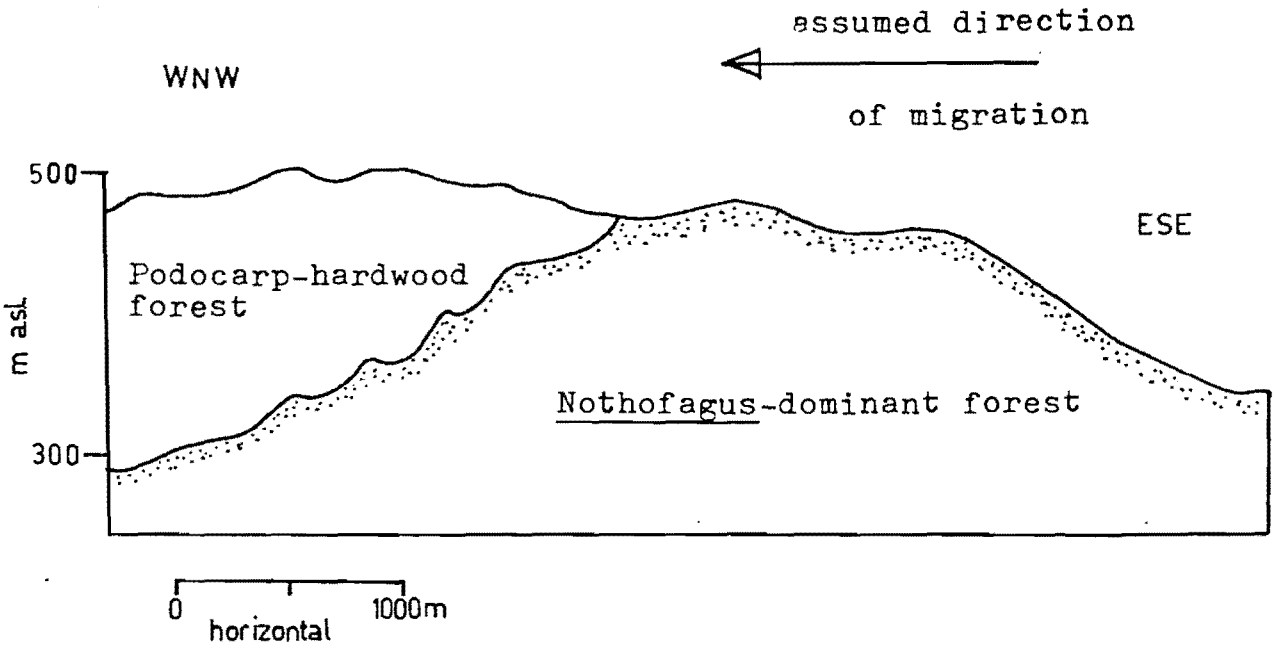


Figure 23: Profile view of Lake Hill Ridge from the south showing the position of the beech forest boundary in relation to topography, and assumed direction of migration.

of the block of hill country is consistent with a predominant migration direction from the north-east and also with migration from the northern, eastern and south-eastern margins of the hill country. Similarly the position of a large podocarp-hardwood forest enclave on the terraces 7 km south of Lake Hochstetter indicates a direction of migration from the east (Figs 10 and 12).

(iv) The distribution of *Nothofagus menziesii* forest on the upper slopes of the southern Paparoa Range (Figs 8 and 9) indicates migration from the north and south of the area not completely occupied by beech forest, and also migration from west to east across the main range at a number of places.

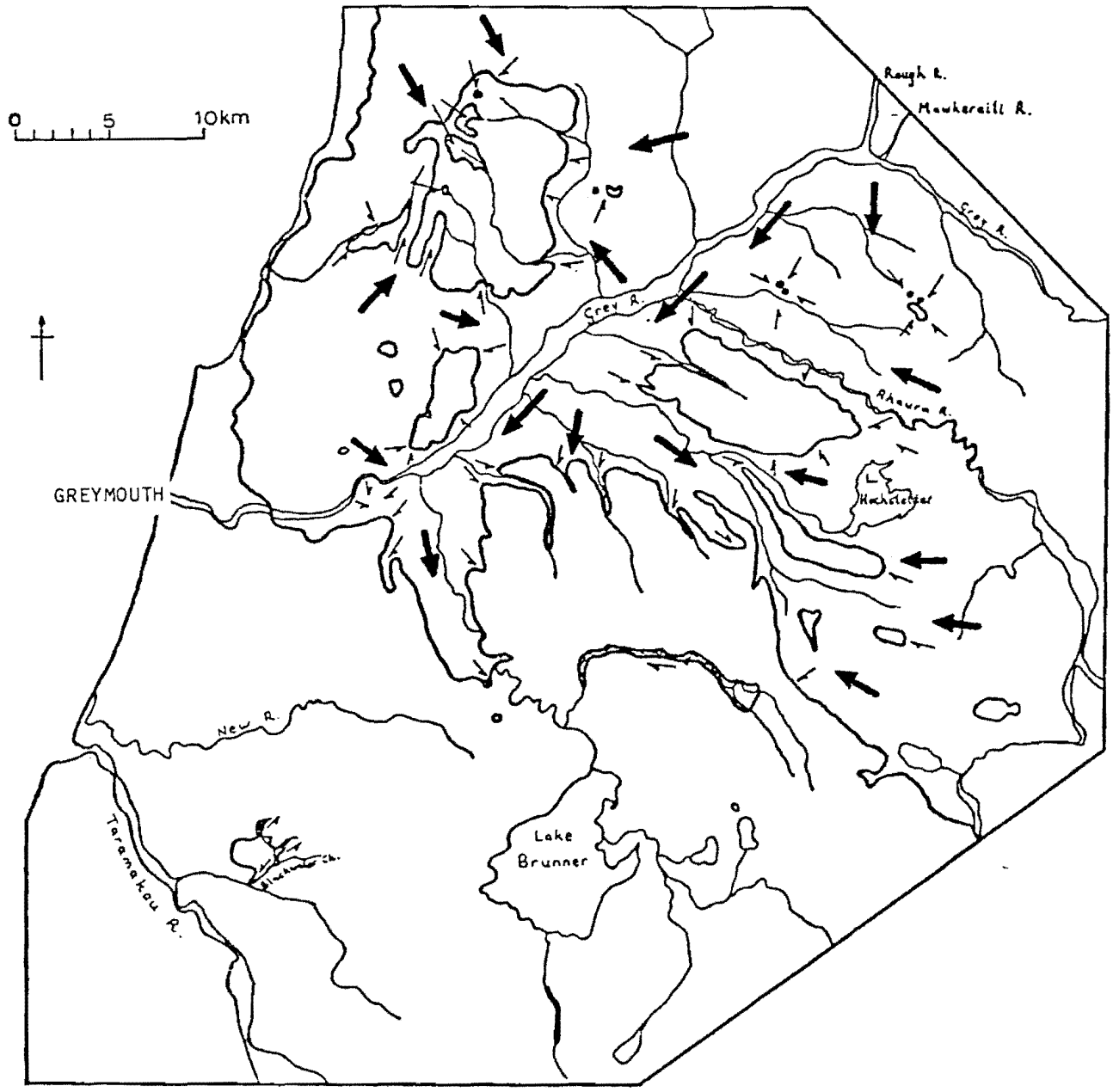
Given the evidence for the frequent concurrence of the fuscoid group species at or near the beech forest boundary (section 4.2.11) and the distributions of the species (Fig 14) it appears that the overall migration directions of these species are similar. On a local level the actual migration route will depend on the ability of each species to occupy different growing sites. In the lowlands, *Nothofagus menziesii* and *N. solandri* var. *cliffortioides* will be more restricted in available routes than *N. truncata* and *N. fusca* because of their inability to occupy hill slopes and particularly ridge crests. These sites will therefore act as minor barriers to migration for *N. menziesii* and *N. solandri* var. *cliffortioides*.

Using the inferred migration directions, which apply to the immediate vicinity of the boundary, and the general topography of the area, the major migration routes in the study area can be identified (Fig 24). These show migration from a number of directions, predominantly from the west, north-east and east. Migration from the north-east follows the course of the Grey River towards the coast with minor routes radiating upstream along the side tributaries. From the west, migration routes extend from coastal areas, across the southern Paparoa Range at a number of places, particularly the low level section adjacent to Blackball, and also around the southern end of the range into the lower Grey and Arnold Valleys. From the east the inferred migration routes

Figure 24 Inferred Nothofagus migration routes in the study area.

migration directions associated with existing boundaries

major migration routes



extend from the rolling terrace country between Haupiri and Waipuna into the central hill country of the Grey Valley and along valleys of westward flowing rivers. Three major directions of migration therefore merge in the centre of the Grey Valley. There is also evidence of both northward and southward migration into the large podocarp-hardwood forest enclave to the north of Blackball.

Outside the study area in the Southern Alps, some migration routes are evident from distribution patterns. These generally follow a southerly or westerly direction and include presumed migration routes extending across the Main Divide from the beech forests of the montane valleys of north Canterbury. The high, non-vegetated mountain ranges in this region, and the scarcity of low passes between the major ridges, are formidable barriers to migration. However, two forested passes, the Lewis Pass (860 m a.s.l.) and the Ada Pass (1000 m a.s.l.) are available as migration routes in the north. Proceeding southwards there are four low passes with subalpine scrub extending through them. These are the Amuri Pass (1010 m a.s.l.), Hope Pass (950 m a.s.l.), Harper Pass (960 m a.s.l. and Worseley Pass (990 m a.s.l.) where scattered *N. menziesii* occurs across the pass (C.J. Burrows, pers. comm.). In the next low pass to the south, Arthurs Pass (920 m a.s.l.), there is a 3.5 km gap between the *N. solandri* var. *cliffortioides* forest on the eastern side and the timberline on the western side, although several small *N. solandri cliffortioides* outliers and areas of subalpine scrub are present in the pass. From the distribution patterns of the *Nothofagus* species on either side of the Main Divide (section 4.2.11) it seems likely that migration by long-distance dispersal has proceeded across the relatively small barrier offered by Worseley Pass into the Otehake valley. Migration across the Amuri, Harpers and Hope Passes is also possible. Arthurs Pass and other higher passes to the north have not served as migration routes.

4.10 POPULATION SIZE STRUCTURES

4.10.1 Complete population size structures

The population structures of the seven major canopy tree species in the study stands are shown in Table 14. In general, each population is dominated numerically by small seedlings (less than 7.5 cm in height) and the frequency of successively older life stages rapidly declines from the small seedling through to the sapling and pole stage. Rata and miro are the exceptions to this pattern. In some rata populations seedling densities are very low and the density of small seedlings may be lower than large seedling densities. Densities of small miro seedlings are lower than large seedling densities because of the rapid early growth rates of this species.

Many of the populations have an overall structure of pyramidal form with lower frequencies in each successive life stage from seedlings to adult canopy trees (Table 14). Hard beech, red beech, Quintinia and kamahi populations, together with at least one of the miro populations studied have this pyramidal form. Rimu, rata and some miro population structures do not conform to this pattern. These populations have deficiencies in the frequencies of seedlings or poles and saplings compared with the pyramidal form. Rata populations generally show greater deficiencies in the younger life stages than the other species in this group. In some rata populations small seedlings are rare and less frequent than large seedlings. The deficiency of saplings and poles in some rata populations (Stands 1 and 2) is more marked than in any of the measured rimu populations.

4.10.2 Size-frequency distribution of subcanopy rimu individuals

The frequencies of subcanopy individuals in successive size classes show a rapid decline with increasing height (Fig. 28). Individuals greater than 2 m in height are infrequent, being present at densities of less than three per hectare for each one metre height class. The most rapid decline in frequency occurs at the 7.5 cm height class.

The frequency distribution for individuals in these three life stages (with canopy trees excluded) is of the pyramidal form.

TABLE 14 Population size structures of canopy tree species (mean numbers of individuals per hectare)

Species and Stand	Small Seedlings[1]	Large Seedlings[2]	Saplings and Poles	Canopy Trees
1. RIMU				
Podocarp-hardwood, Stand 1	5300 (0.53 ± 0.73/m²)	120 (50-180)	9.3	22.3
Podocarp-hardwood, Stand 2	n.s.	190 (130-260)	9.3	17.6
Podocarp-hardwood, Stand 3C	9100 (0.91 ± 1.55/m²)	1060 (420-1700)	24	61
Beech-podocarp, Stand 3C	8400 (0.84 ± 1.35/m²)	170 (90-250)	10	69
Beech-podocarp, Stand 9	300 (0.03 ± 0.18/m²)	10	0.7	0.7
Beech-podocarp, Stand 5	200 (0.02 ± 0.12/m²)	10	3.7	2.8
2. MIRO[3]				
Podocarp-hardwood, Stand 1	infrequent	1150 (590-1710)	6.7	11.6
Podocarp-hardwood, Stand 2	infrequent	n.s. (infrequent)	1.8	0.9
Padocarp-hardwood, Stand 3C	infrequent	1090 (560-1620)	11.5	6.6
Beech-podocarp, Stand 3C	infrequent	n.s.	8	8
Beech-podocarp, Stand 9	infrequent	n.s. (infrequent)	5.0	0.0
Beech-podocarp, Stand 5	infrequent	n.s. (infrequent)	0.0	0.9

TABLE 14 (cont'd)

Species and Stand	Small Seedlings[1]	Large Seedlings[2]	Saplings and Poles	Canopy Trees
3. RATA				
Podocarp–hardwood, Stand 1	n.s.	240 (40–440)	0.9	53.0
Podocarp–hardwood, Stand 2	n.s.	n.s.	2.8	58.3
Podocarp–hardwood, Stand 3C	3500 (0.35 ± 1.52/m²)	390 (80–700)	30.2	101.4
Beech–podocarp, Stand 3C	500 (0.05 ± 0.31/m²)	670 (410–930)	77	24
Beech–podocarp, Stand 9	0	40	3.3	0
Beech–podocarp, Stand 5	100	100 (0–230)	20.4	0
4. HARD BEECH				
Beech–podocarp, Stand 3C	64920 (6.49 ± 6.45/m²)	30290 (8510–52070)	590	117
Beech–podocarp, Stand 9	85700 (8.57 ± 9.78/m²)	12410 (3260–21560)	1791	180
5. RED BEECH				
Beech–podocarp, Stand 5	14200 (1.42 ± 2.45/m²)	2130 (1060–3560)	152.8	56.5
6. KAMAHI				
Podocarp–hardwood, Stand 1	very abundant	3260 (1690–4830)	964	428
Podocarp–hardwood, Stand 3C	"	n.s.	n.s.	405
Beech–podocarp, Stand 3C	"	n.s.	n.s.	317

TABLE 14 (cont'd)

Species and Stand	Small Seedlings[1]	Large Seedlings[2]	Saplings and Poles	Canopy Trees
7. QUINTINIA				
Podocarp–hardwood, Stand 1	very abundant	18990 (9350–28630)	2405	545
Podocarp–hardwood, Stand 3C	"	n.s.	n.s.	246
Beech–podocarp, Stand 3C	"	n.s.	n.s.	142

Sample areas are described in Table 5.

n.s. = not sampled

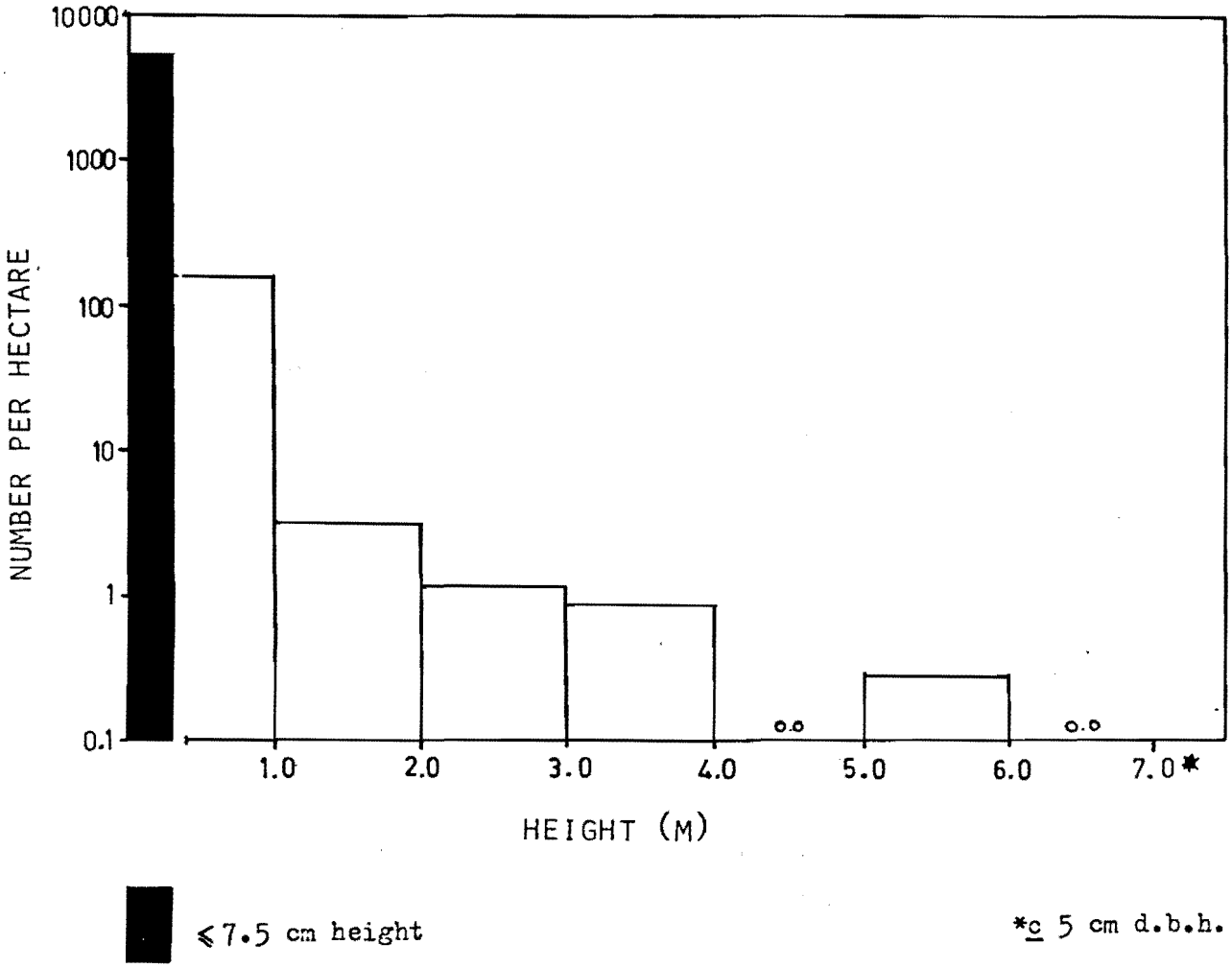
[1] Mean sample densities with standard deviations are in brackets.

[2] 95% confidence limits of the mean are in brackets.

[3] Most miro seedlings grow taller than 7.5 cm in their first or second year. Few seedlings (1% in a sample of 457) were taller than 50 cm.

All stands except for Stand 3C are on ridge crests and mid hill slopes. Stand 3C covers lower slopes.

See Table 4 for descriptions of study stands.



For individual >1 m tall, the total area sampled was 4.53 hectares. Sampling methods are described in section 3.9

Figure 28: Size-frequency distribution for rimu subcanopy individuals (small seedlings, large seedlings and saplings) in Stand 1 and 2.

4.10.3 Size-frequency distributions for saplings, poles and canopy trees (all species)

Stem diameter-frequency distributions for all individuals in a population greater than 1 m in height are shown in Figs 29, 30, 31, 32, 33 and 34. For rimu, Figure 29 shows data for populations in podocarp-hardwood stands on hill slopes and Figure 30 shows data for populations in podocarp-hardwood stands on high and intermediate outwash terraces and populations in beech-podocarp stands on hill slopes. Combined stand data for rimu are used in Figure 31 to give a comparison of size frequency-distributions between populations on terrace and hill slope sites. The data from the low density populations in beech-podocarp forest (Fig. 30) are not adequate to show a reliable frequency distribution.

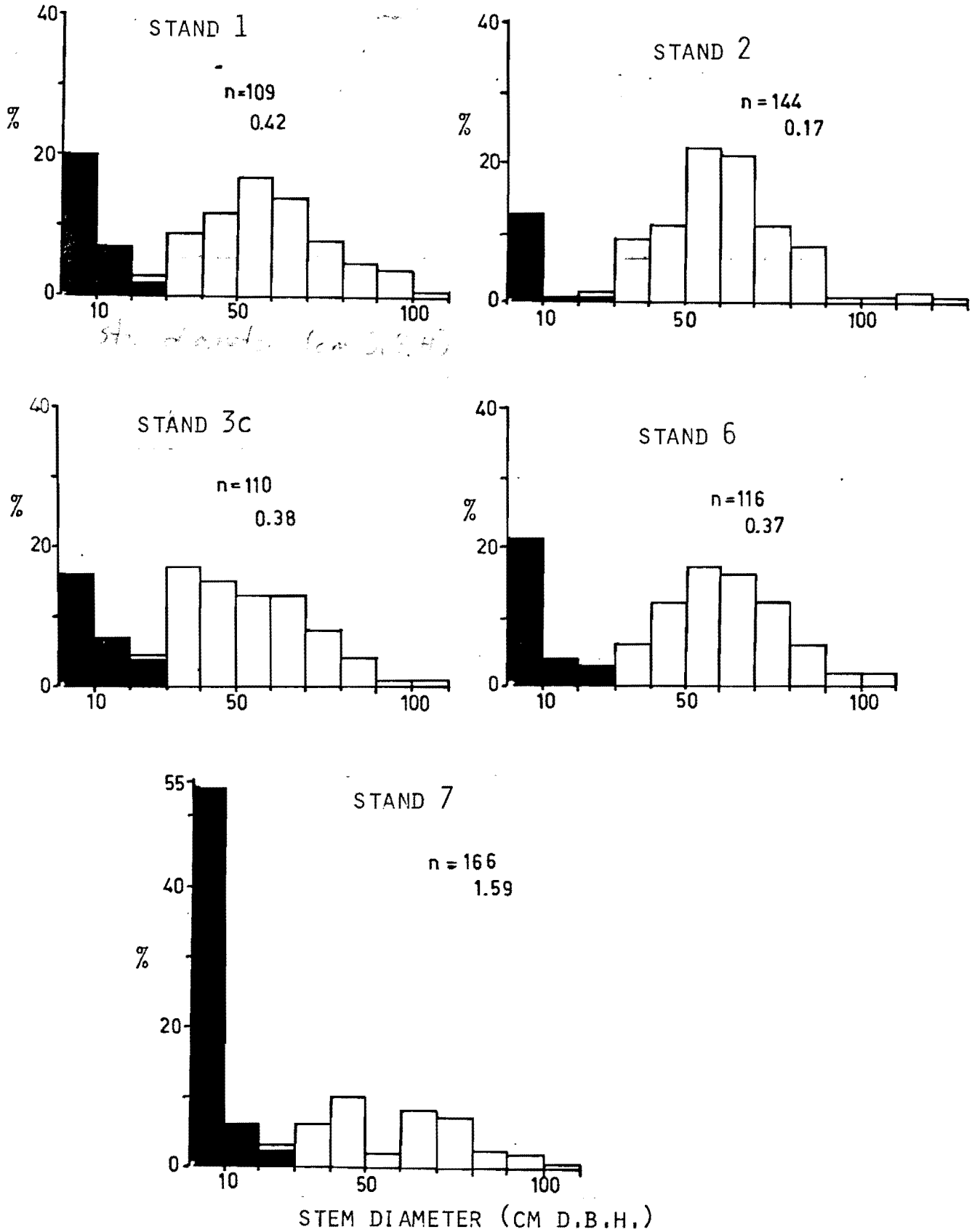
The frequency distributions for rimu have a characteristic bimodal form. One modal peak occurs in the smallest size class (less than 10 cm d.b.h. and comprising saplings and poles up to about 10 m in height). The second peak occurs in the 50-60 cm or 60-70 cm d.b.h. size classes in hill slope populations and in the 30-40 or 40-50 cm d.b.h. size classes in terrace populations. Apart from the largest size classes, the lowest frequencies are found in the 10-30 cm d.b.h. range between the two modal peaks. Individuals in this size range are close to the height of the hardwood canopy or just above it.

Compared with an exponential frequency distribution based on the larger size classes, the populations are deficient in the smaller size classes and can be said to exhibit a 'regeneration gap' (cf. Fig. 3).

Observations in undisturbed forests throughout the Grey Valley indicate that a similar, bimodal population size structure is present in all localities and over the whole altitudinal range of rimu. There is, however, some variability in population structure from place to place. For example, the ratio of subcanopy to canopy individuals varies from 0.17 in Stand 2 to 1.59 in Stand 7 (Fig. 29). Other stands with a higher than average proportion of smaller individuals are found in the Lisbon Creek area (see Fig. 4 and Table 4). At the other extreme, saplings and poles are rare in the near-coastal hill country in the Aorangi Scenic Reserve (see Fig. 4 and Table 4).

A comparison with population structures on glacial outwash terraces (Figs 29, 30 and 31) shows that on terrace sites canopy trees

Figure 29: Size-frequency distributions for rimu saplings, poles and canopy trees at different locations (hill slopes; podocarp–hardwood stands). (Shaded portions indicate subcanopy individuals ⩾ 1 m tall. The ratio of subcanopy to canopy individuals is shown next to the sample size).



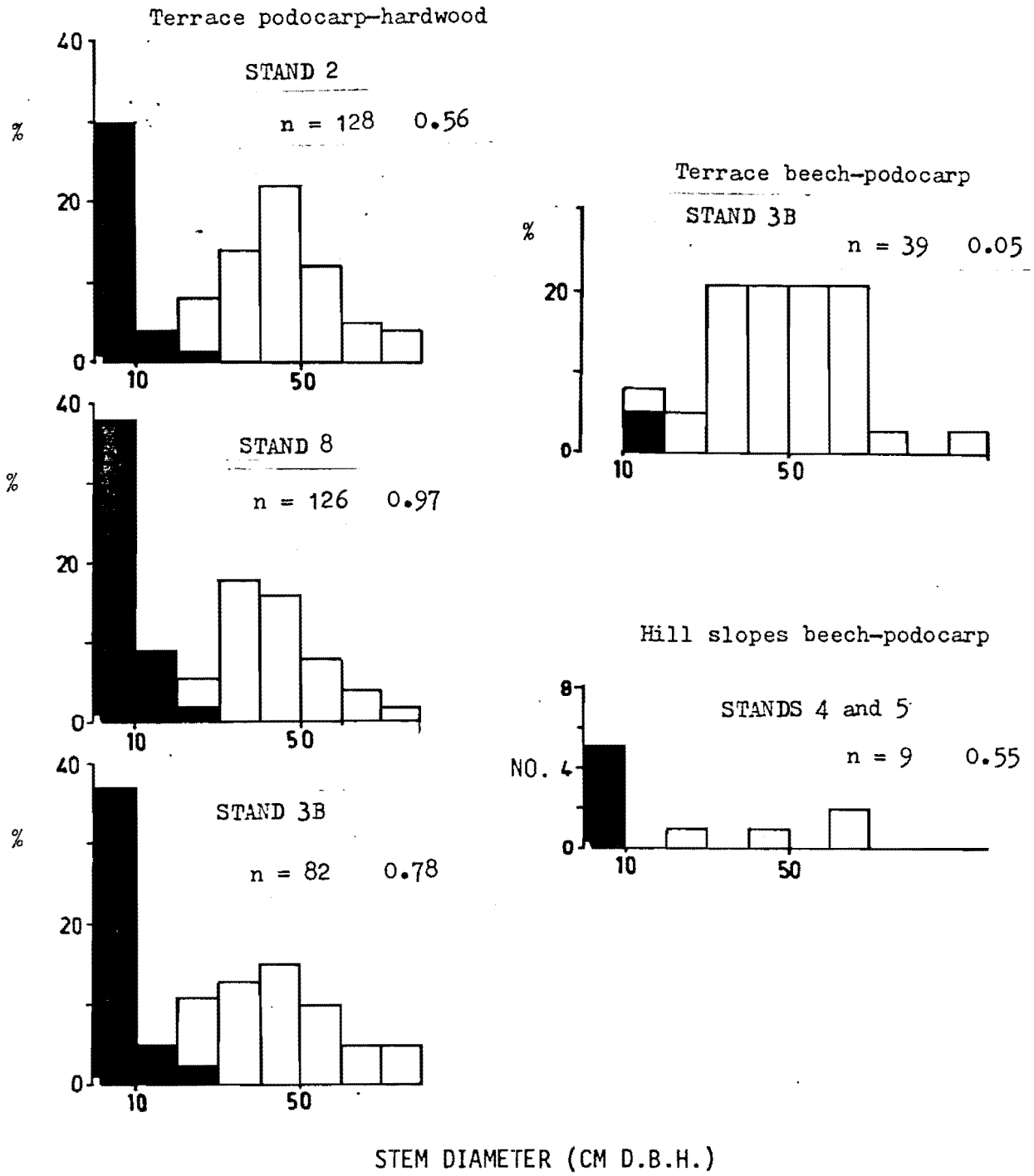
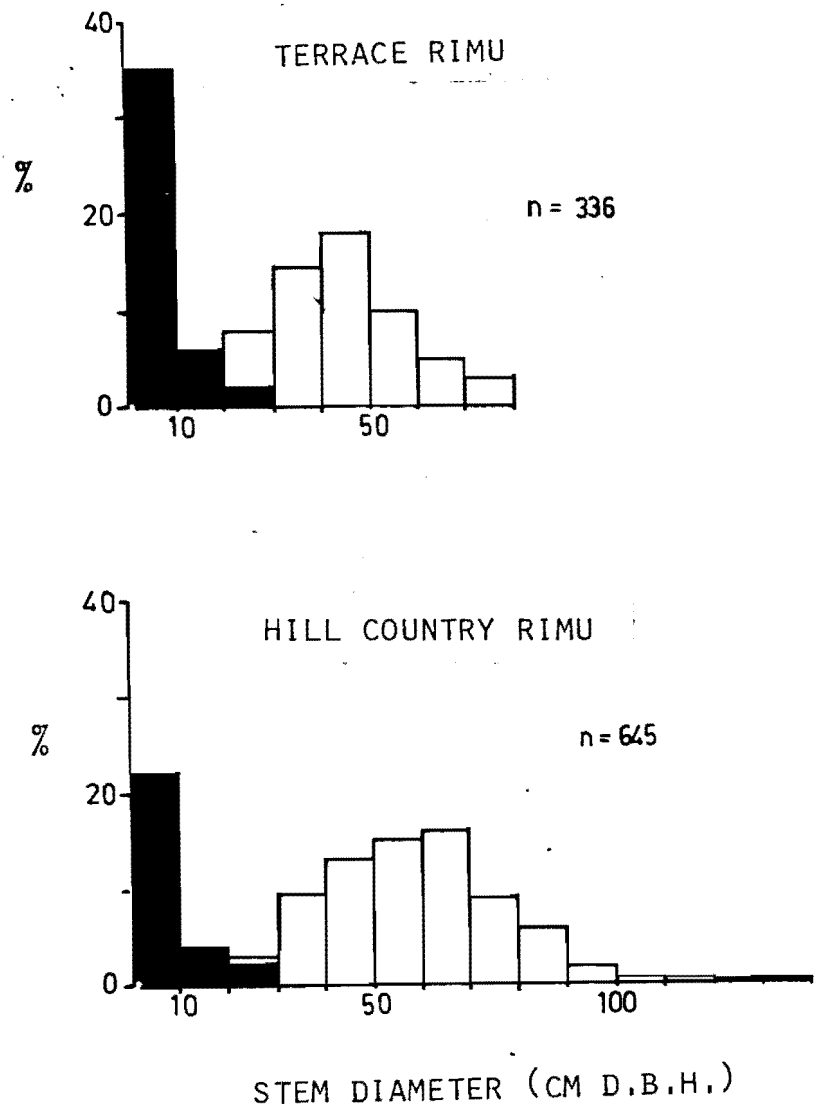


Figure 30: Size-frequency distributions for rimu saplings, poles and canopy trees (terrace sites and beech-podocarp stands). (Shaded portions indicate subcanopy individuals ≥ 1 m tall. The ratio of subcanopy to canopy individuals is shown next to the sample size).



(Shaded portions indicate subcanopy individuals ≥1 m tall).

Figure 31: A comparison of size-frequency distributions for rimu saplings, poles and canopy trees in podocarp-hardwood forest on hill slopes and outwash terraces (combined stand data from Figs 29 and 30).

reach a smaller maximum size and there is a higher proportion of saplings and poles in the population. On terrace sites the decline in the frequency-distribution between the two modal peaks (i.e. the 'regeneration gap') is less pronounced.

Other species

The other species (Figs. 32, 33 and 34) show much variability in population structure. A bimodal size-frequency distribution, similar to the distributions for rimu, is found in miro and some rata populations (Fig. 32). In other rata populations the frequency distribution is unimodal with low or zero frequencies for the smallest size classes. The frequency distributions for red beech (Fig. 33) also show a 'regeneration gap', but with a relatively high frequency of saplings and poles under 10 cm d.b.h.

In contrast to rimu, rata, miro and red beech, the remaining species, hard beech, Quintinia and kamahi, have size-frequency distributions of the J-shaped form (Figs 33 and 34).

4.10.4 Tree diameter growth rates

The relationships between stem diameter and estimated age are shown for rimu in Figure 35, for red beech, hard beech, rata and miro in Figure 36 and for Quintina and kamahi in Figure 37. The data presented are predominantly for canopy trees, and do not adequately show growth rates for subcanopy individuals (saplings and poles) except in the case of rimu.

The relationship between stem diameter and estimated age for rimu is a variable one, although there is a relatively strong correlation between size and age for subcanopy trees less than 10 cm d.b.h. (Fig.35). With larger diameters, the correlation between age and stem size weakens. Thus, for example, individuals greater than 60 cm d.b.h. with the same diameter may differ in age by as much as 700 years. For large trees stem size cannot be used as a reliable indicator of age. A high degree of variability is also evident in the size-age relationships of the other canopy tree species (Figs 36 and 37), although, as for rimu, the linear regressions fitted to the data are highly significant. This means that size structures based on diameter-frequency distributions cannot be interpreted in detail as age structures.

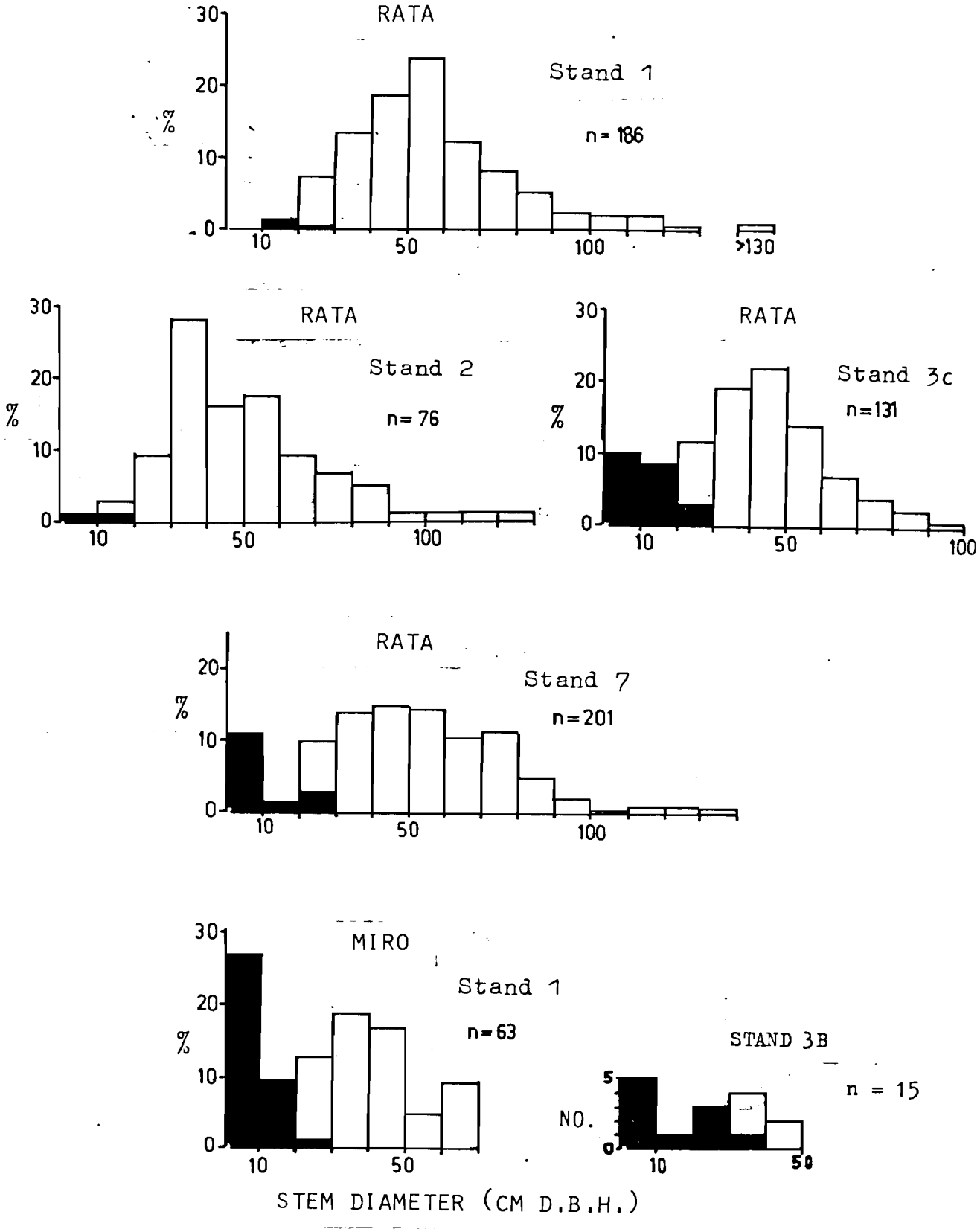


Figure 32: Size-frequency distributions for rata and miro saplings, poles and canopy trees. (All stands are in podocarp–hardwood forest).
Shaded portions indicate subcanopy individuals ≥ 1 m tall.
All stands are on hill slopes except 3B.

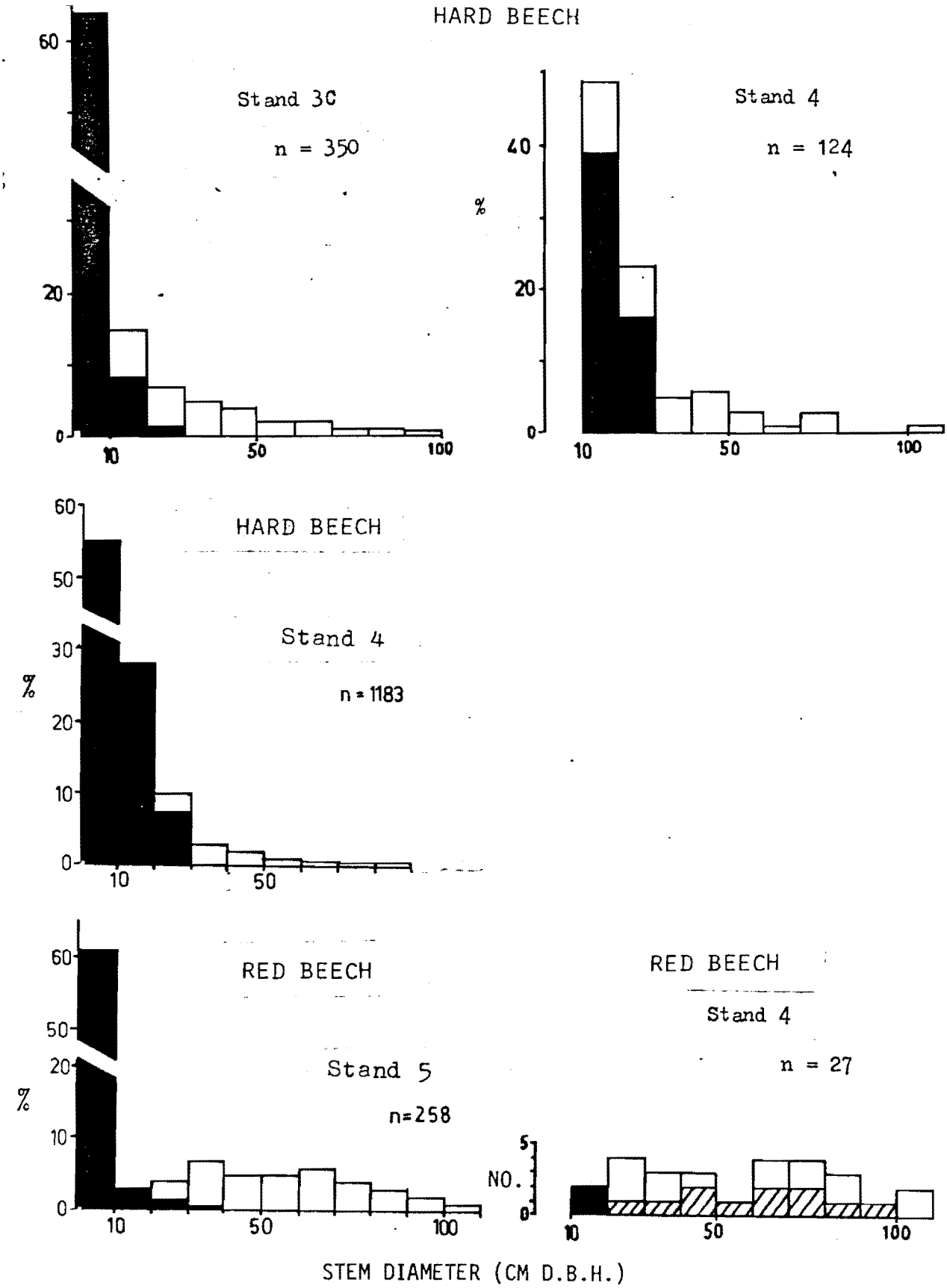


Figure 33: Size-frequency distributions for hard beech and red beech saplings, poles and canopy trees.
Shaded portions indicate subcanopy individuals ⩾ 1 m tall.
Cross-hatched portions in red beech indicate recently dead trees.

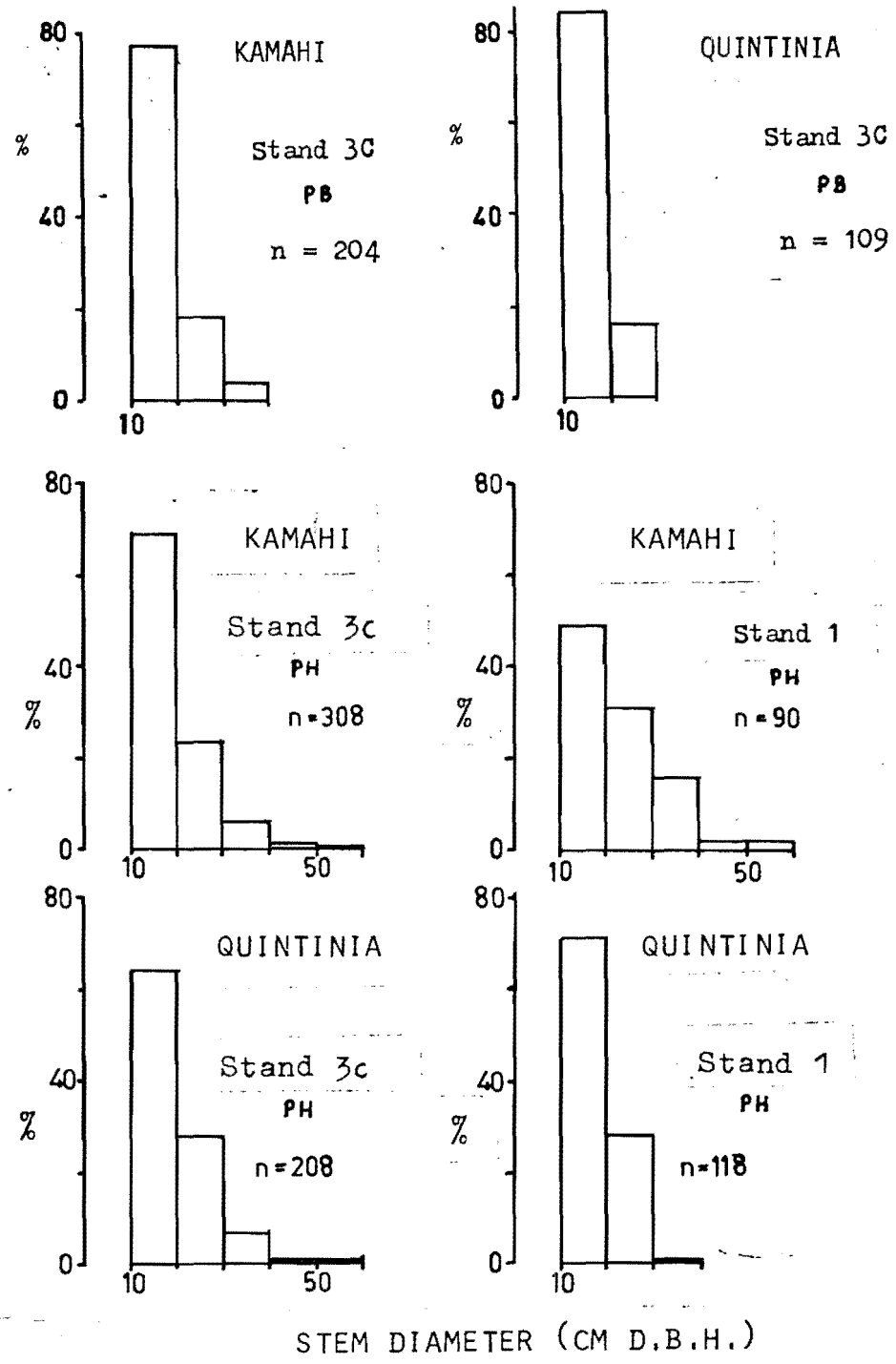
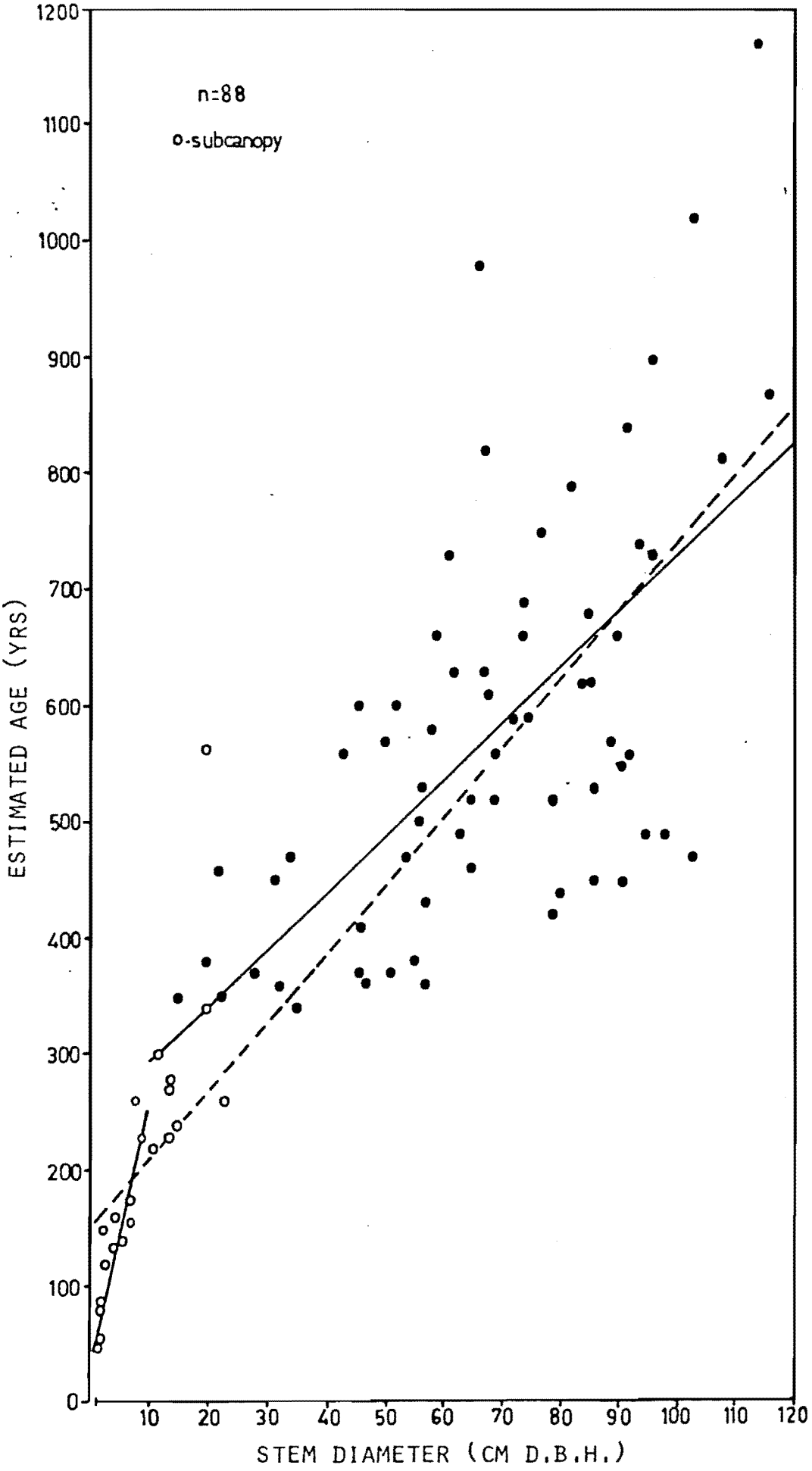


Figure 34: Size-frequency distributions for kamahi and Quintinia saplings, poles and canopy trees.

(PB = beech-podocarp forest; PH = podocarp-hardwood forest)

Figure 35. The age-stem diameter relationship for rimu saplings (>2 m tall), poles and canopy trees. The relationship can be described by the linear regression $y = 6.01x + 135$, $r = 0.82$, $P < 0.01$ (dotted line); for individuals < 10 cm d.b.h. by $y = 21.64x + 44$, $r = 0.78$, $P < 0.01$; for individuals > 10 cm d.b.h. by $y = 4.84x + 243$ $r = 0.70$, $P < 0.01$ (solid lines).


n=88
o-subcanopy
ESTIMATED AGE (YRS)
STEM DIAMETER (CM D.B.H.)
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
10
20
30
40
50
60
70
80
90
100
110
120

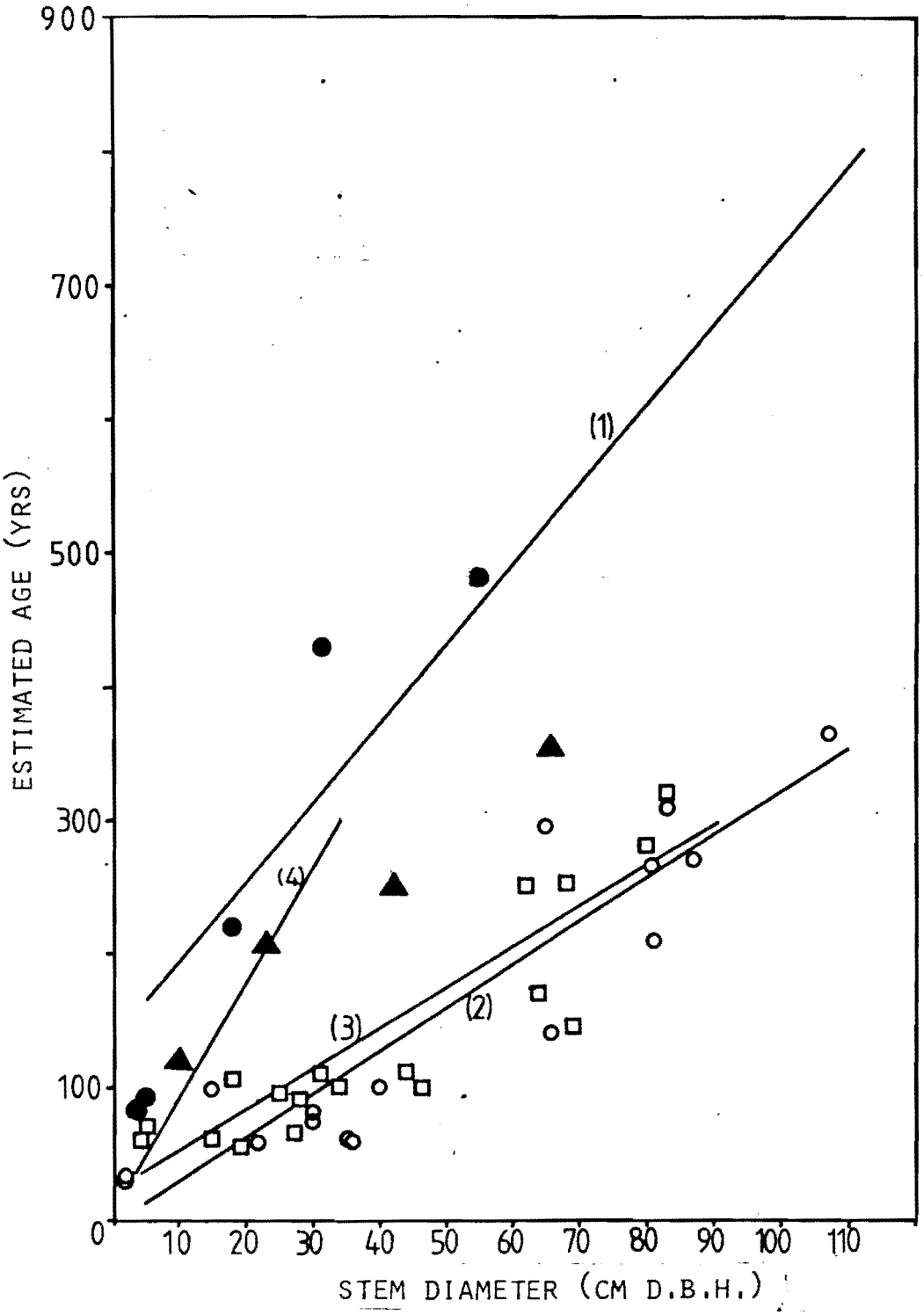


Figure 36. Age-stem diameter relationships for seven canopy tree species

(1) rimu (from Fig. 35)

(2) ○ red beech y = 3.23x - 4, r = 0.93, P < 0.01

(3) □ hard beech y = 3.04x + 21, r = 0.74, P < 0.01

(4) *Quintinia* and kamahi (from Fig. 37)

▲ rata

● miro

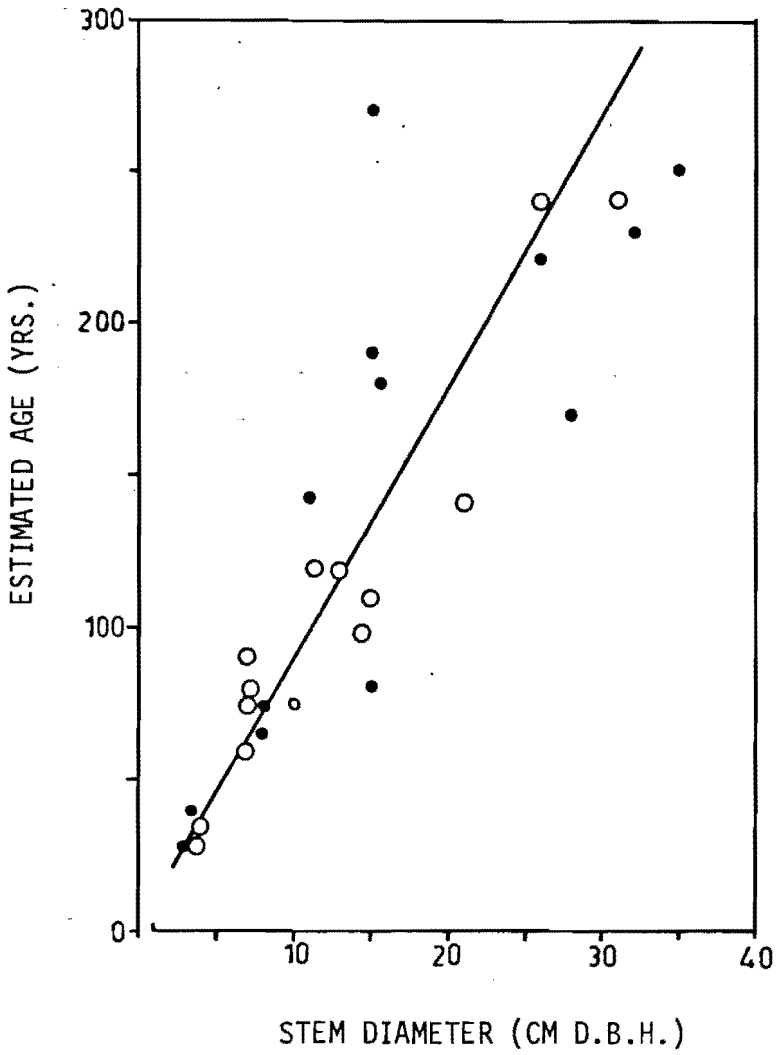


Figure 37: Age-stem diameter relationships for Quintinia and kamahi. (open circles - Quintinia; closed circles - kamahi)

The size-age relationship is, however, sufficiently reliable to allow general conclusions to be drawn about the population age structure, or the relative ages of different trees on the basis of observed tree diameters. The error in absolute terms in the predicted age of a tree on the basis of diameter will be less for the shorter-lived species and more for rimu which appears to have the longest life span of the seven species studied.

The beech species have the most rapid diameter growth rates and rimu and miro the slowest. The data for miro and rata and inadequate to derive a fully reliable diameter-age relationship but the four estimates for each of the two species indicate growth rates for miro similar to and for rata faster than rimu growth rates. Diameter growth rates of Quintinia and kamahi are relatively slow.

4.10.5 Rimu population age structures

The general form of the complete population age structures can be derived from the size structures (Table 14) using the age ranges of each life stage. The most striking feature is the rapid decline in frequencies within the 5-10 year age range.

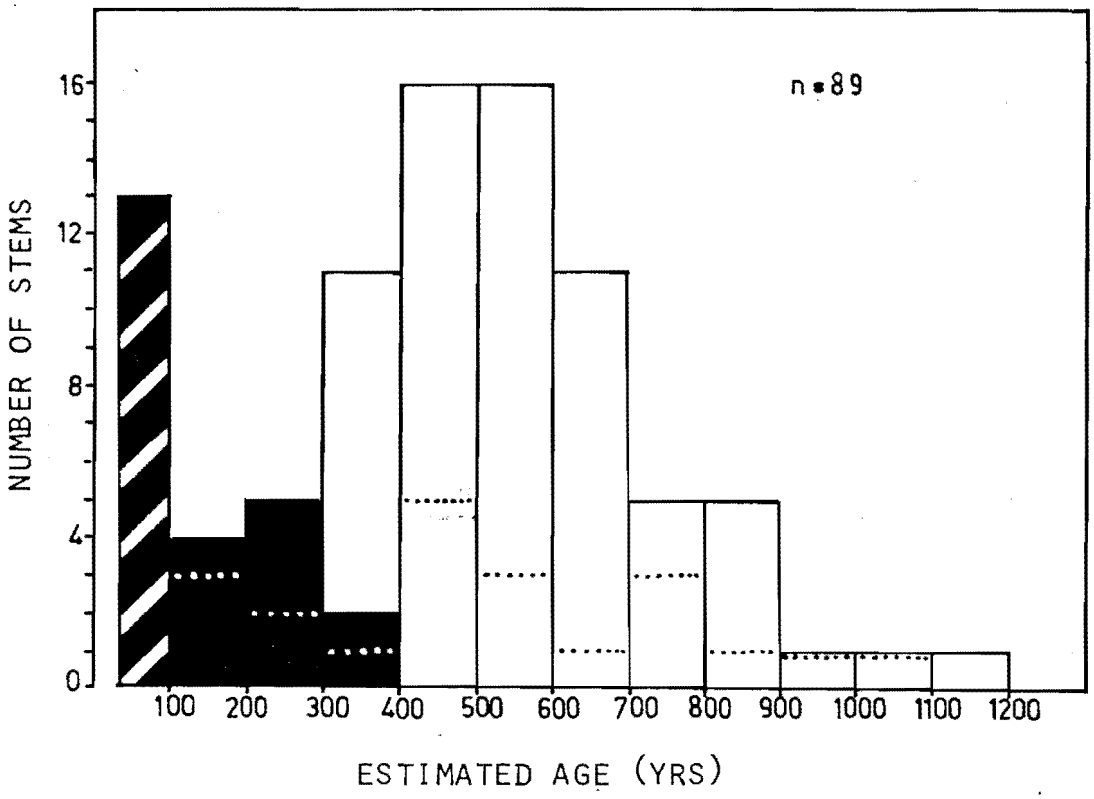
A detailed age structure for rimu canopy trees and subcanopy trees older than c. 25 years (greater than 1 m in height) is shown in Fig. 38. Data from the two stands sampled were combined in order to obtain an adequate sample size for a frequency distribution. Like the size structures (Fig. 29), the age structure is bimodal. Most trees are between 400 and 600 years of age and the oldest individual in the sample was estimated to be 1170 years old.

The general form of the age structure is similar to the size structures from the stands sampled (Fig. 29). This confirms that size structures can be interpreted in general terms as a proxy for age structures despite the variability in the age-stem diameter relationship (Fig. 35).

4.10.6 A model for the predicted input of rimu individuals into the 100-200 year and 200-300 year age classes at different periods of time

Purpose of the model

The model aims to compare rates of regeneration at different



Shaded portions are subcanopy trees greater than 1 m tall. Cross-hatched column was derived indirectly from the size-frequency distributions and age data (see section 3.10).

Individuals below the dotted lines are from Stand 6, the remainder from Stand 1.

Figure 38. An age structure for rimu (Dacrydium cupressinum)

periods within the past 400 years. This is done by obtaining estimates of the input into the various age classes at different periods, using the present age-frequency distribution in Stands 1 and 6 (Fig. 38) and allowing for mortality losses and growth over the appropriate periods.

Assumptions

A number of assumptions are made about age and mortality rate estimates and these are described in turn.

The minimum age limit of 25 years for the youngest age class was derived indirectly from the age-height relationship (Fig. 40). This age represents the extreme limit; most individuals would be about 40 years of age at 1 m tall. Using both these minimum age estimates, it is assumed that all individuals will pass out of the youngest age class (which has a maximum age of 100 years) in 60 to 75 years. If it is also assumed that individual ages are evenly distributed within the age class, then the mean residence time in the age class will be half the age range, i.e. 30 to 37.5 years.

Mortality is assumed to be density-independent among saplings and poles. The estimated mortality rate for saplings and poles was 0.8% p.a. (section 4.12). Because of the uncertainties of this estimate, a mortality rate 50% higher, i.e. 1.2% p.a. and one 50% lower, i.e. 0.4% p.a., were used as alternatives in the model. A further assumption is that the two stands sampled have the same population history. The data from each stand are inadequate for separate analyses.

Calculations and results

The predicted output from the 13 individuals in the 25–100 year age class (Fig. 38) can be calculated using the two estimates of mean residence time and the three mortality estimates. Mortality is compounded annually throughout the mean residence period.

Thus, for a mean residence time of 30 years, predicted output

$$= \frac{13(1-0.004)^{30}}{30} = 0.38 \text{ p.a. (0.4\% p.a. mortality),}$$

$$\text{or } \frac{13(1-0.008)^{30}}{30} = 0.34 \text{ p.a. (0.8\% p.a. mortality),}$$

$$\text{or } \frac{13(1-0.012)^{30}}{30} = 0.32 \text{ p.a. (1.2\% p.a. mortality);}$$

and for a mean residence time of 37.5 years, predicted output

$$= \frac{13(1-0.004)^{37.5}}{37.5} = 0.30 \text{ p.a. } (0.4\% \text{ p.a. mortality}),$$

$$\text{or} \quad \frac{13(1-0.008)^{37.5}}{37.5} = 0.24 \text{ p.a. } (0.8\% \text{ p.a. mortality}),$$

$$\text{or} \quad \frac{13(1-0.012)^{37.5}}{37.5} = 0.22 \text{ p.a. } (1.2\% \text{ p.a. mortality}).$$

These predicted outputs are equivalent to inputs into the next oldest (100-200 year) age class. The predicted outputs can be compared with the input rate which gave rise to the present number of individuals in the 100-200 year class. Assuming that the four individuals in the class have had a mean residence time of 50 years (half the class age interval) and allowing for compounded annual mortality, then the past input rate

$$= \frac{4}{(1-0.004)^{50}.50} = 0.10 \text{ p.a. } (0.4\% \text{ p.a. mortality}),$$

$$\text{or} \quad \frac{4}{(1-0.008)^{50}.50} = 0.12 \text{ p.a. } (0.8\% \text{ p.a. mortality}),$$

$$\text{or} \quad \frac{4}{(1-0.012)^{50}.50} = 0.15 \text{ p.a. } (1.2\% \text{ p.a. mortality}).$$

A comparison of the two sets of input/output data indicates that input rates into the 100-200 year age class are likely to be up to two to four times the rate in the next 30-37.5 years compared with the past 100 years.

A similar analysis can be made with the 200-300 year age class in which five individuals are present (Fig. 38). The input at an equivalent period to that calculated for the 100-200 year age class is estimated by using a mean residence time of 150 years. The same mortality rates are used. The input rate

$$= \frac{5}{(1-0.004)^{150}.150} = 0.06 \text{ p.a. } (0.4\% \text{ p.a. mortality}),$$

$$\text{or} \quad \frac{5}{(1-0.008)^{150}.150} = 0.11 \text{ p.a. } (0.8\% \text{ p.a. mortality}),$$

or $$\frac{5}{(1-0.012)^{150} \cdot 150} = 0.20 \text{ p.a. } (1.2\% \text{ p.a. mortality}).$$

These input rates are only slightly higher or lower than for the 100–200 age class.

The relatively high frequency in the 300–400 year age range (11 individuals) shows that previous input rates for this age class must have been higher than for the younger age classes.

In general terms the model suggests that recruitment rates during the last 100 years (specifically within the past 25–100 years) have been about two to four times as high as during the period from 100 to 300 years ago, and that the recruitment rates 100 to 200 years ago were about the same as those 200 to 300 years ago. Recruitment rates in the period from 300 to 400 years ago appear to have been greater than during any more recent period.

4.11 SEEDLING POPULATION DYNAMICS

4.11.1 Seedling densities

Red beech, hard beech, Quintinia and kamahi were found to have high to very high seedling densities in the study stands (Table 14). Densities of up to 85 700/ha for seedlings less than 7.5 cm tall were estimated for hard beech, for example. Rata and miro seedling densities are relatively low and of similar magnitude to rimu seedling densities. These species have seedling densities in the order of 10/ha to 1200/ha. There are more small seedlings than large seedlings except for the rata populations in beech-podocarp stands where small seedling densities are very low.

Many of the Quintinia and kamahi individuals in the seedling classes have arisen by vegetative reproduction (epicormic shoots or root suckers). Vegetative reproduction was not observed in the other species.

A comparison of rimu and rata seedling densities in podocarp-hardwood and beech-podocarp stands on comparable sites (see Table 14) shows that seedling densities are mostly lower in the beech -podocarp forest type. For rimu, there is an approximately 10-fold difference in large seedling densities between forest types. For rata populations, the differences are not as great and not as consistent and in Stand 3 large rata seedling densities are higher in the beech-podocarp forest type.

4.11.2 Early establishment rates

The numbers of newly-established seedlings were counted in late winter of each year of assessment. These counts represent the numbers of newly germinated seedlings which have survived through to the beginning of their second growing season. The rates of establishment of rimu, rata, miro, hard beech and red beech in permanent quadrats over the whole period of observation, are shown in Table 15. The beech species have the highest establishment rates with the equivalent of 22 000 seedlings/ha of hard beech seedlings establishing per year over the three years from 1974 to 1977 and 8 600 seedlings/ha/yr red beech seedlings establishing over the same period. Mean rimu establishment rates over this period were 3 400 seedlings/ha/yr. The rates of

TABLE 15. Densities and establishment, mortality and outgrowth rates of small seedlings in permanent quadrats (data averaged over the two or three year period of measurement).

Species and Stand		Establishment Rate ($no/m^2/yr$)	Average Density (no/m^2)	Mortality Rate ($no/m^2/yr$)	Net Outgrowth Rate ($no/m^2/yr$)
Rimu:	3A	0.65	2.05	0.41	0.07
	3C	0.19	1.34	0.14	0.03
	5	0.11	0.86	0.04	0.0
	3B	0.34	1.62	0.47	0.06
	4A	0.52	2.23	0.30	0.04
	4B	0.16	0.51	0.08	0.04
Sample Mean		0.34	1.45	0.24	0.04
Miro:	3A	0.02	0.13	0.06	0.03
	3C	0.0	0.0	0.0	0.0
	5	0.0	0.07	0.0	0.01
	3B	0.0	0.08	0.0	0.0
	4A	0.06	0.27	0.04	0.10
	4B	0.06	0.21	0.06	0.02
Sample Mean		0.02	0.13	0.03	0.03
Rata:	3A	0.02	0.18	0.0	0.0
	3C	0.25	2.41	0.09	0.03
	5	0.0	0.03	0.0	0.0
	3B	0.04	0.16	0.02	0.0
	4A	0.0	0.04	0.0	0.0
	4B	0.02	0.17	0.02	0.0
Sample Mean		0.06	0.49	0.02	0.005
Hard Beech:	3A	1.74	6.40	0.71	0.54
	3C	0.89	4.38	0.78	0.31
	3B	3.19	4.20	0.24	0.12
	4A	4.04	12.36	1.55	2.00
Sample Mean		2.21	6.77	0.79	0.66
Red Beech:	5	0.58	2.17	0.39	0.11
	4B	1.27	2.27	0.70	0.21
Sample Mean		0.86	2.22	0.51	0.15

Seedling numbers, summarized by stand, are shown in Appendix IV

establishment were low for rata, with a mean rate of 600 seedlings/ha/yr. Establishment rates for miro were very low at 200 seedlings/ha/yr. Establishment rates are generally proportional to seedling densities (Table 15).

Establishment rates vary considerably from year to year, particularly for red and hard beech (Figure 39). In 1975 no new hard beech seedlings were recorded, but two years later following heavy seed production in the previous summer the rate of establishment was equivalent to 4.20 seedlings/m^2. Red beech showed a similar trend from year to year, but the annual fluctuations in rimu show an opposing trend with the highest rate of establishment recorded in 1975 and the lowest in 1977. Data for miro and rata are not adequate to describe annual trends.

4.11.3 Microsite preferences

Although seedlings germinate on a wide variety of microsites on the forest floor, some microsites are more favourable than others for seedling survival. The most favourable microsites are moss colonies (which are common on the ground and on rotten logs) and areas where the litter is thin or where the humus or mineral layers of the soil are exposed at the surface. The exposed surfaces in the depression caused by the uplifting of the root system of a windthrown tree is a particularly favourable microsite. Rotten wood surfaces and animal tracks where the litter has been compacted are also favourable. Small seedlings fail to survive in areas occupied by dense colonies of fern (usually Blechnum spp.) and are infrequent in areas where the litter layer is deep or where the ground is covered by Metrosideros perforata, M. diffusa and herbaceous species.

There are significant species differences in the microsite preferences of small seedlings. First year seedlings of red beech, hard beech and miro are able to survive in thicker litter layers than the other species, which are capable of relatively less height growth during the cotyledonary stage and early growing seasons. Miro seedlings are able to establish in deep litter as well as other types of microsite. On flat, terrace sites rimu seedlings show a marked preference for the edges of small, water-filled depressions on the ground surface. The other species do not establish on this microsite.

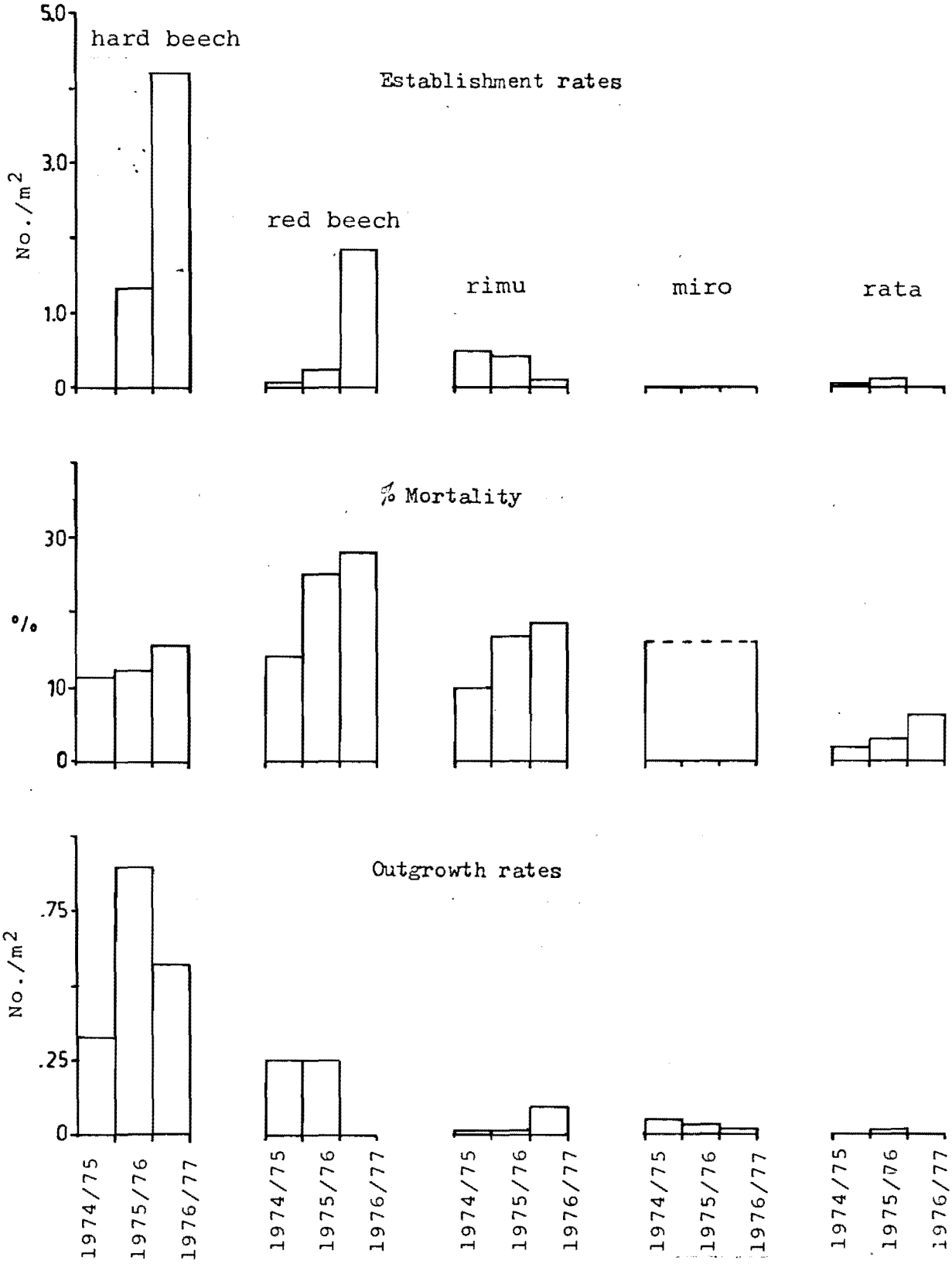


Figure 39: Annual rates of establishment, mortality and outgrowth of small seedlings in permanent quadrats.

The microsite preferences of small seedlings of rimu, rata, hard beech and red beech in four categories of permanent quadrats are shown in Table 16. Rata seedlings have the greatest specificity in microsite preferences with 97% of the seedlings in the log-canopy gap microsite. Red beech and rimu also show some preference for the log microsite. Hard beech seedlings show the lowest degree of microsite specificity, but still have a significant preference for microsites on the ground and without a low subcanopy foliage layer. For all four species, seedlings are less common than expected where there is a low shrub layer (compared with similar microsites lacking this layer). There are more rimu seedlings on ground microsites under a canopy than expected ($P < 0.05$) and fewer rata and hard beech seedlings than expected ($p < 0.01$) on the same microsites. For the same microsite in a canopy gap there are fewer rata seedlings than expected ($P < 0.01$) and more hard beech seedlings than expected ($P < 0.01$). These results for the bare ground microsite together indicate a preference for microsites beneath a canopy in the case of rimu seedlings and a preference for microsites in canopy openings in the case of hard beech.

TABLE 16 Microsite preferences of small seedlings in permanent quadrats, showing seedling frequencies.

	Microsite				Totals
	ground, under canopy	log, canopy gap	Shrub layer canopy gap	ground, canopy gap	
rimu	162*	199**	59**	129	549
rata	0**	195**	5**	2**	202
Hard beech	133**	182	166	263**	744
Red beech	28	68**	6**	18*	120

Superscripts refer to the results of individual χ^2 tests : *$P < 0.05$; ** $P < 0.01$; the remainder are not significant.
Expected frequencies for each microsite are 137.25 for rimu, 50.5 for rata, 186 for hard beech, 30 for red beech.

Newly-established rimu and rata seedlings appear to be more vulnerable to desiccation in exposed situations (for example, in large canopy gaps with a sparse shrub layer) than the other species. The beech species, Quintinia and kamahi are able to establish more readily in canopy gaps where they form seedling clumps of high density. Quintinia and kamahi are also able to reproduce vegetatively from existing damaged or intact trees in a gap and this ability contributes to their prolific establishment in gaps.

On the basis of observations on seedling microsites, the tolerances of small seedlings to the competitive effects of overshadowing trees and shrubs take the following order: miro>rimu, rata, red beech and hard beech>kamahi and Quintinia. Large seedlings occupy a more restricted range of microsites than small seedlings. Thus, many seedlings establish in situations where further development is inhibited or prevented. There are two microsites where large seedlings of rimu, rata and miro are absent or rare; beneath dense clumps of Quintinia, kamahi and beech seedlings and saplings in canopy gaps, and around the base of canopy trees. It appears, however, that large rimu seedlings are able to develop beneath the canopy of rata trees.

Fallen, rotting logs and stumps and the mounds and depressions resulting from the windthrow of large trees are particularly favourable microsites for large rimu, rata and hard beech seedlings. Rimu seedlings also show a preference for the margins of water-filled depressions on terrace sites. These preferred microsites are not common. Large seedlings are also found on litter or moss-covered areas throughout most of the study stands.

4.11.4 Mortality

Mortality rates of small seedlings were assessed in permanent quadrats over a two or three year period. For large seedlings, mortality was estimated from a sample of tagged seedlings. Mortality rates of small seedlings are lowest for rata (4.0% p.a.) and highest for red beech (23.3% p.a.), see Table 17.

TABLE 17 Mortality of small seedlings in permanent quadrats, showing seedling frequencies summed over the years of observation.

Species	Dead	Live	Total	% mortality p.a.
Rimu	90	459	549	16.4
Miro	10	53	63	16
Rata	8	194	202	4.0
Hard Beech	99	645	744	13.3
Red Beech	28	92	120	23.3

From individual X^2 tests between the species the following result was obtained. Species' mortality rates which are not significantly different ($P > 0.05$) are joined by a line; all other differences are significant at the 1% level:

Rata Hard Beech Miro Rimu Red Beech

Annual mortality rates for small seedlings were lowest in the period 1974/75 and highest in the period 1976/77. The overall yearly differences (for all species combined) are significant ($X^2 = 8.75$, $P < 0.05$); the period 1974/75 with 9.4% mortality has a significantly lower rate of mortality than 1975/76 with 13.9% mortality ($X^2 = 4.16$, $P < 0.05$) and the period 1976/77 with a mortality of 16.3% has a rate which is not significantly different from the previous year ($X^2 = 1.40$, $P > 0.05$). An increasing rate of mortality from 1974/75 to 1976/77 was observed for each species, although the trend is not a significant one ($P > 0.05$) for any species individually.

The effects of microsite on small seedling mortality are shown in Table 18. The highest mortality rates (21.7% p.a. for all species) were generally found in the bare ground microsite under a canopy and the lowest (9.2% p.a. for all species) on the log microsite in a canopy gap. The data for rata are too few for a realistic analysis of microsite effects. For rimu seedlings the differences in mortality rate between the bare ground under-canopy and the log-canopy microsite are significant ($X^2_1 = 8.24$, $P < 0.05$), but other differences between microsites are not significant ($P > 0.05$).

TABLE 18 Mortality rates of small seedlings in permanent quadrats on different microsites, showing % mortality p.a.

Species	Microsite				X^2_3
	ground, under canopy	log, canopy gap	shrub layer, canopy gap	ground, canopy gap	
Rimu	22.8	11.6	15.3	16.3	8.31, P<0.05
Rata	0	4.1	0	0	-
Hard Beech	17.3	7.7	16.9	12.9	8.64, P<0.05
Red Beech	36	21	0	22	4.59, n.s.
All species	21.7	9.2	15.7	14.3	29.00, P<0.01

For hard beech seedlings, the microsite effects can be summarized in the following table (non-significant, P>0.05, differences are underlined):

log–canopy gap	ground–canopy gap	shrub–canopy gap	ground–canopy

The mortality rates of rimu and rata small seedlings in the two forest types are shown in Table 19.

TABLE 19 Mortality rates of small seedlings in permanent quadrats in different forest types, showing seedling frequencies.

Species and forest type	Dead	Live	Total	% mortality p.a.	X^2_1
Rata: beech–podocarp	1	3	4	25	-
podocarp–hardwood	7	191	198	3.5	
Rimu: beech–podocarp	44	169	213	20.7	4.64
podocarp–hardwood	46	290	336	13.7	(P<0.05)

The mortality rate is significantly lower for small rimu seedlings growing in podocarp-hardwood forest compared with beech-podocarp forest. Data for rata (and miro) seedlings are insufficient for analysis.

Mortality rates for tagged populations of rimu, rata, miro, hard beech and red beech large seedlings are described in Table 20.

TABLE 20 Mortality of large seedlings in tagged populations, showing seedling frequencies summed over the years of observation.

Species	Dead	Live	Total	% mortality p.a.
Rimu	31	976	1007	4.1
Miro	12	492	504	2.4
Rata	13	1006	1019	1.3
Hard Beech	60	1151	1211	5.0
Red Beech	6	300	306	2.0

From individual X^2 tests between species, the differences which are not significantly different at the 5% level are underlined below:

rata red beech miro rimu hard beech

Rata, red beech and miro seedlings have the lowest mortality rates (from 1.3% p.a. to 2.4% p.a.) and hard beech the highest mortality rate (5.0% p.a.). For each species, mortality rates of large seedlings are considerably lower than mortality rates of small seedlings. The relative differences between the species have also changed for small and large seedlings. For example, red beech had the highest mortality rate (23.3% p.a.) among small seedlings but one of the lowest mortality rates (2.0% p.a.) among large seedlings. Both small and large rata seedlings have the lowest mortality rates for all species.

Mortality rates of large seedlings did not vary significantly ($P>0.05$) from year to year during the period of measurements and there were no consistent trends between species from year to year.

Mortality rates of large seedlings on different microsites are shown in Table 21. For each species, mortality rates do not vary

TABLE 21 Mortality rates of large seedlings in tagged populations on different microsites, showing % mortality p.a.

Species	Microsite				X^2_3
	Under canopy		In canopy gap		
	ground	log	ground	log	
Rimu	2.8	1.7	3.6	4.0	2.37 n.s.
Miro	3.4	3.5	1.1	1.5	2.71 n.s.
Rata	0.9	2.6	0.5	1.2	2.06 n.s.
Hard Beech	5.3	4.3	6.2	3.7	2.89 n.s.
Red Beech	5	0	2	1.2	3.52 n.s.

X^2_3 = 7.81 for P = 0.05. n.s. = not significant at the 5% level. The X^2 tests were performed using numbers of live and dead seedlings as in previous tests. These data are not shown here.

significantly ($P > 0.05$) between microsites. However, when results from both microsites under a canopy and in canopy gaps are combined, there is a significant difference ($X^2_1 = 6.31$, $P < 0.05$) in the mortality rates of large miro seedlings under a canopy cover (5.6% p.a.) and in canopy gaps (1.2% p.a.). Rimu seedlings show an opposite effect with lower mortality (2.3% p.a.) under a canopy cover compared with a 3.8% p.a. mortality rate in canopy gaps. This difference is not significant ($P > 0.05$). The effects of microsite on mortality are greater for small seedlings than large seedlings (c.f. Table 18).

Large seedling mortality rates of rimu, rata and miro are not significantly different ($P > 0.05$) between forest types and there are no consistent trends for all species (Table 22).

TABLE 22 Mortality rates of large seedlings in tagged populations in different forest types, showing seedling frequencies

Species and forest type	Dead	Live	Total	% Mortality p.a.	X^2_1
Rimu: beech-podocarp	12	467	479	2.5	1.01, P>0.05
podocarp-hardwood	19	509	528	3.6	
Miro: beech-podocarp	7	238	245	2.9	0.49, P>0.05
podocarp-hardwood	5	254	259	1.9	
Rata: beech-podocarp	3	482	485	0.6	3.20, P>0.05
podocarp-hardwood	10	524	534	1.9	

$X^2_1 = 3.84$ for P = 0.05

Rimu and rata seedlings have lower mortality rates in beech-podocarp forest and miro seedlings lower rates in podocarp-hardwood forest.

Causes of mortality

There are various causes of mortality, some of which are difficult to identify. Among small seedlings, mortality is commonly caused by smothering by litter, uprooting by litter-feeding birds and desiccation during dry periods particularly in exposed situations in canopy gaps. Browsing of small seedlings was rarely observed (except in Stand 5 where goats were present) and no damage by insect predators was observed.

Most deaths among large seedlings occur after a period of suppressed growth when height growth is negligible or when the stems and foliage are subject to dieback. The incidence of growth stagnation and dieback was not evidently related to the density of the overhead canopy; suppressed seedlings were more common under a canopy than in canopy gaps, however. Occasionally, seedlings were killed by falling branches and trunks or by animal browsing. In the limited areas where goats are present, for example Stand 5, browsing can eliminate most seedlings in places such as ridge tops which are frequented by these animals.

4.11.5 Height growth rates

The ages at which seedlings of the different species reach the 7.5 cm and 100 cm height class limits can be seen in Figures 40, 41, 42 and 43. Rimu seedlings reach the 7.5 cm height class in about 5–10 years, miro seedlings in one to five years, rata in four to eight years, red beech in two to six years and hard beech in two to seven years. Growth rates in the small seedling stage appear, therefore, to have the following order of increasing growth rate: rimu < rata < hard beech < red beech < miro. The age ranges at which seedlings reach the 100 cm height class is shown in Table 35, section 4.13.3.

The age-height relationship is generally a variable one (Figures 40, 41, 42 and 43). Growth rates are generally slower in the smaller height classes and increase as seedlings reach the large seedling stage.

The numbers of seedlings growing from the small seedling to the large seedling stage in the permanent quadrats are shown in Fig. 39 and Table 15. The outgrowth rate for each species is proportional to the establishment rate , except that miro has a higher outgrowth rate than expected. Hard beech had the highest net outgrowth rate (mean of 0.66 seedlings/m^2/yr) and rata the lowest (mean of 0.01 seedlings/m^2/yr) over the two or three year period of observation. Annual fluctuations in the outgrowth rate do not show a consistent trend between species. These fluctuations may reflect the level of establishment recorded in an earlier year, for example, a zero rate of outgrowth in red beech in 1976/77 follows three years after a low rate of establishment in 1975. The period of observation may, however, be too short to determine adequately the relationship between the rate of establishment in one year and outgrowth rates in subsequent years.

Annual height growth increments were examined in detail in the tagged large seedlings. Mean annual growth rates take the following order of increasing growth rate: rimu < miro < hard beech < rata < red beech (Table 23).

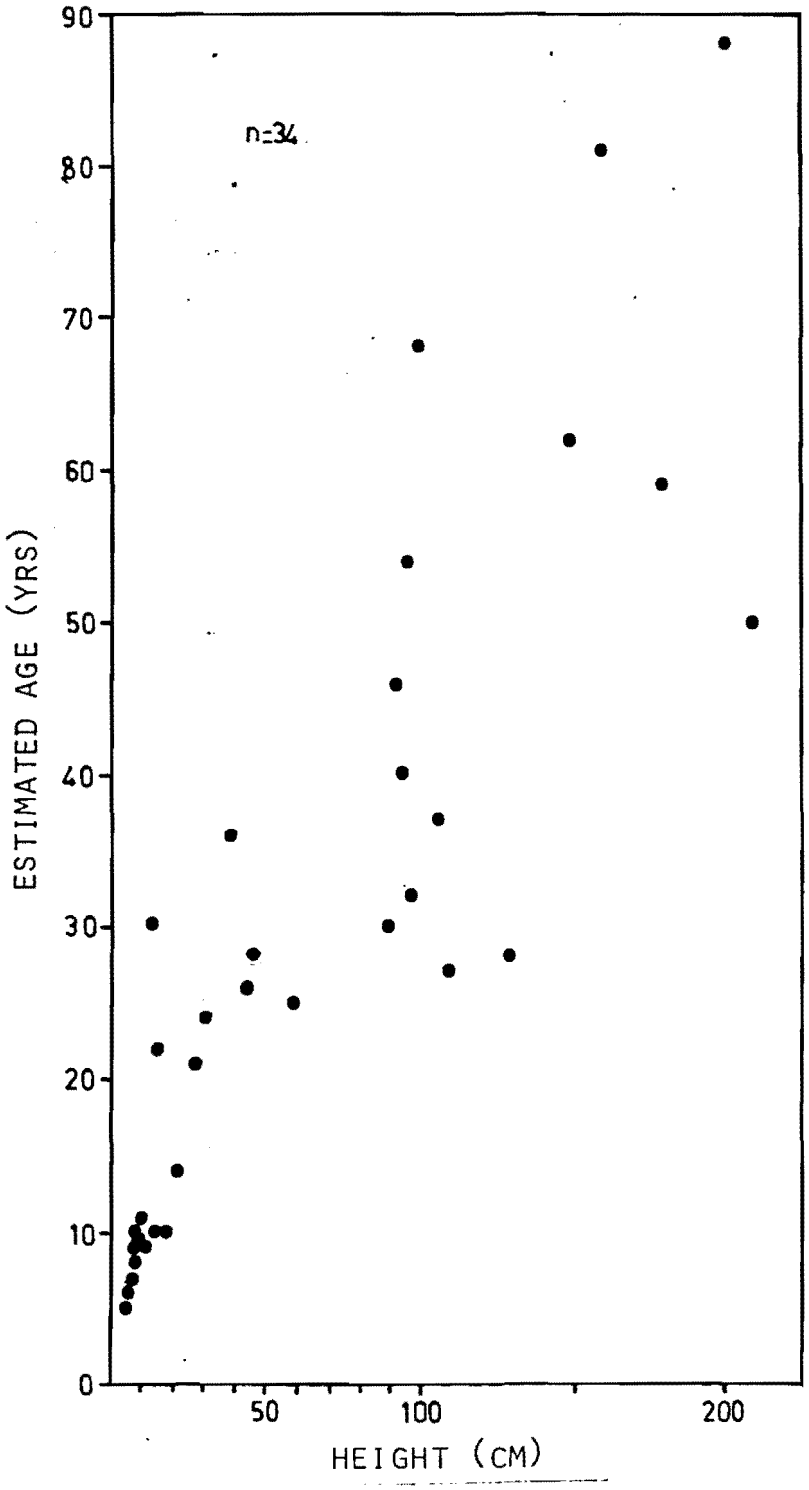


Figure 40. Age-height relationship for rimu seedlings and saplings (the relationship can be described by the linear regression $y = 29.55 \log_{10}x - 16.9$, $r = 0.80$, $P < 0.01$).

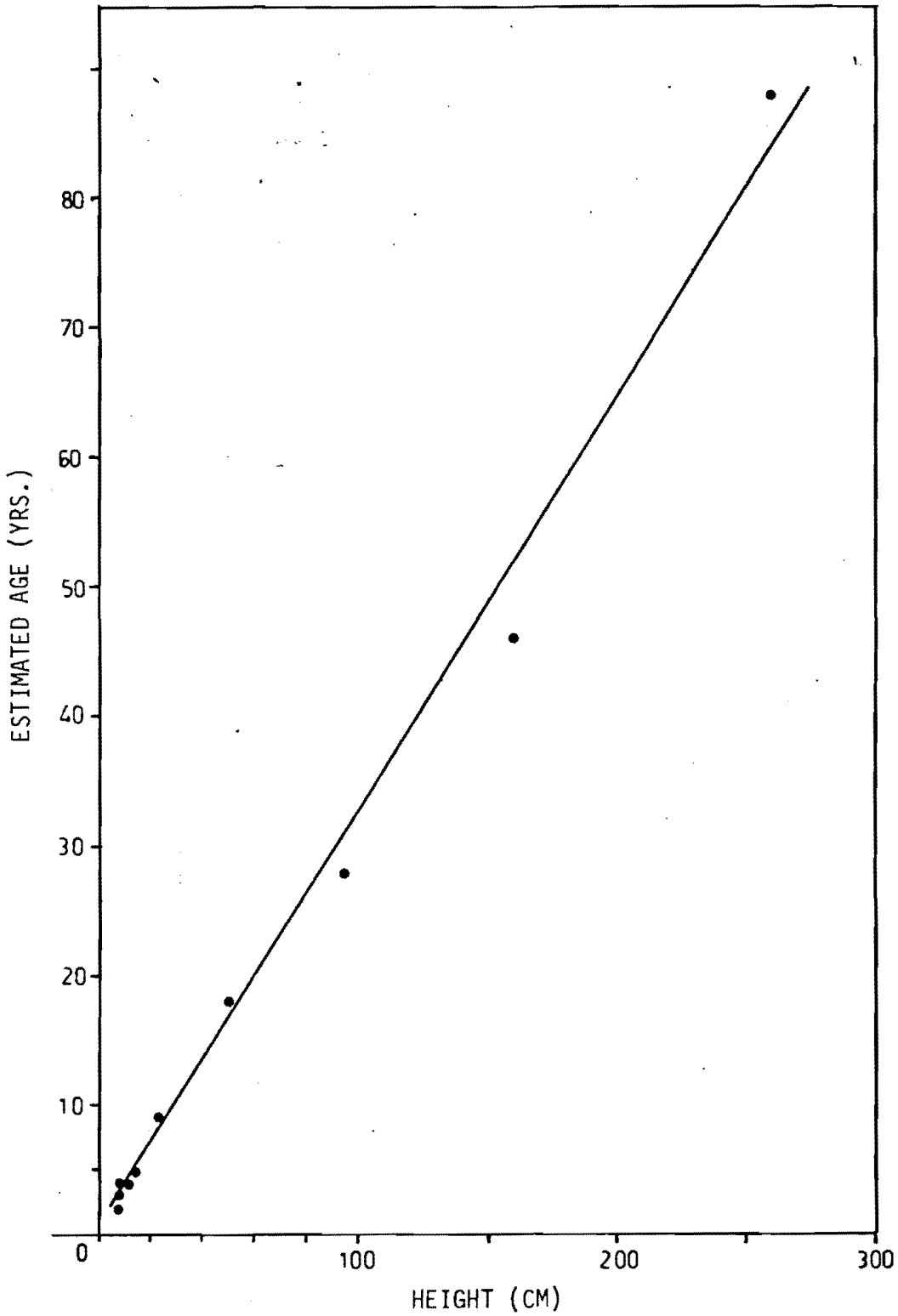


Figure 41: Age-height relationship for miro seedlings and saplings.

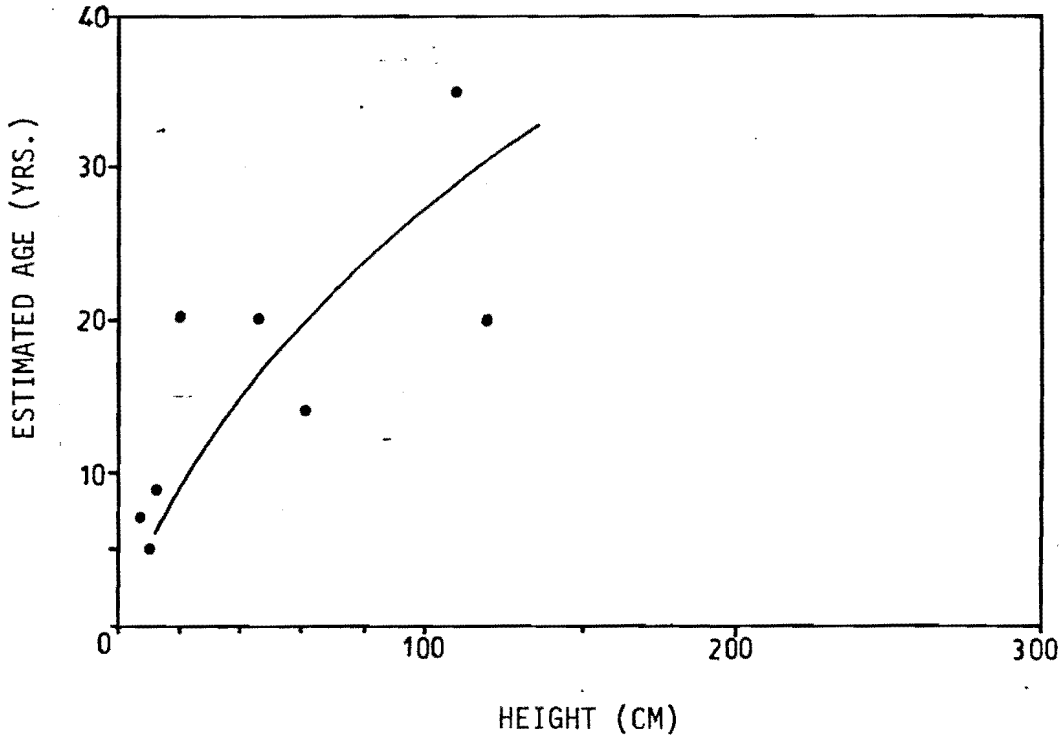
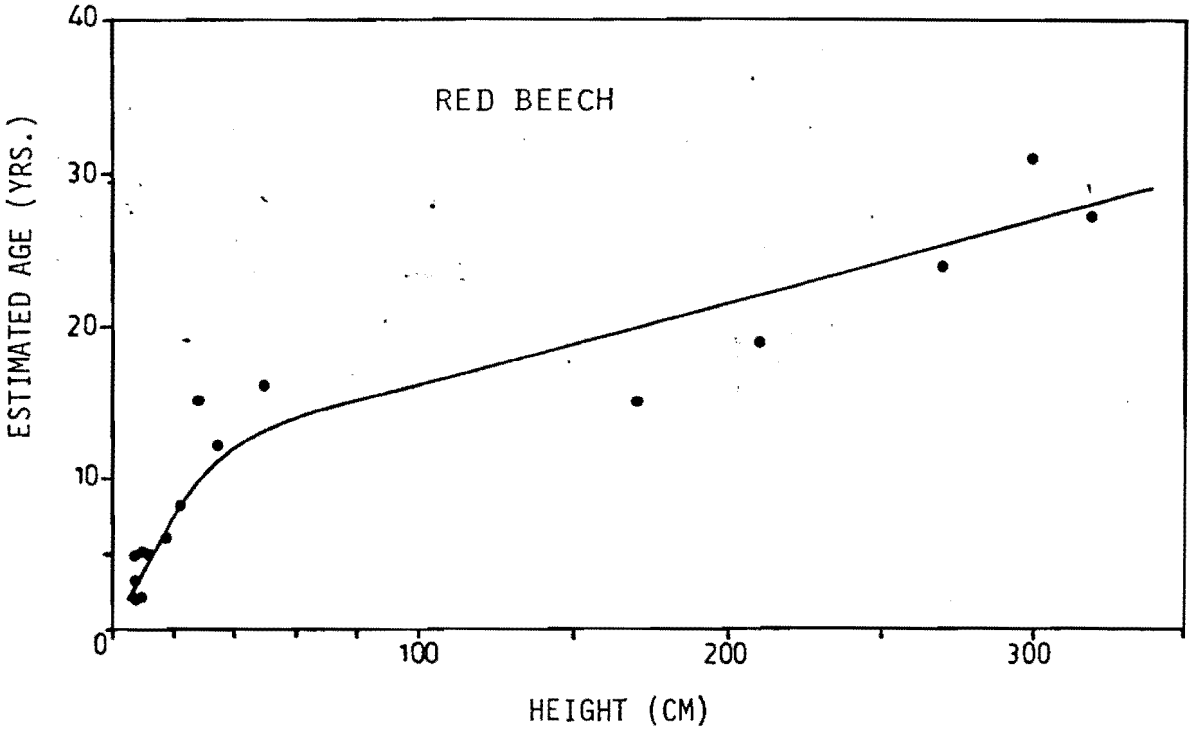


Figure 42: Age-height relationship for rata seedlings and saplings.



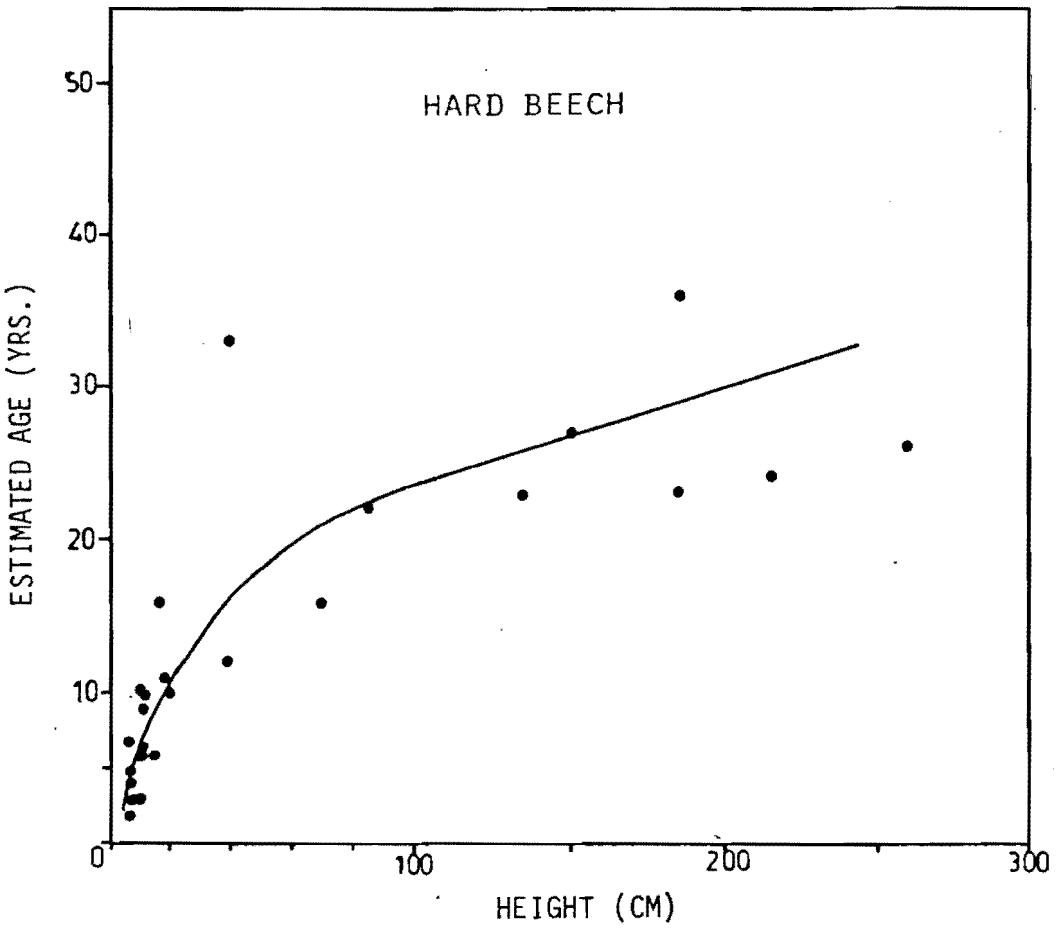


Figure 43: Age-height relationship for red beech and hard beech seedlings and saplings.

TABLE 23 Mean annual height growth rates of large seedlings, ranked by magnitude

	Species				
	Rimu	Miro	Hard beech	Rata	Red Beech
Mean growth rate (cm/yr)	0.81	0.86	1.43	1.47	3.65
Standard deviation of the mean	±1.024	±1.098	±1.941	±1.750	±4.285
No. of seedlings	416	179	282	419	131

The results of multiple comparisons among means using the Student-Newman-Keuls test can be summarized as follows (ranges underlined are not significant at the 5% level):

Rimu	Miro	Hard beech	Rata	Red Beech

For large rimu seedlings there is no evidence of significant variation in growth rate between forest types and microsites (Table 24). Differences in growth rates of seedlings growing in different stands are also not significant.

Seedlings growing in canopy gaps have a slightly faster mean growth rate (0.87 cm/yr) than seedlings growing under a canopy (0.74 cm/yr), but the differences are not significant (Table 24).

TABLE 24 Height growth rates of large rimu seedlings in different forest types, microsites and sites, showing mean growth rates (cm/yr)

Microsite	Forest Type		
	beech-podocarp	podocarp-hardwood	both types
log, under canopy	0.73	0.59	0.74
ground, under canopy	0.79	0.81	
log, canopy gap	0.92	0.68	0.87
ground, canopy gap	0.86	0.96	
Group means	0.82	0.80	

TABLE 24 (cont'd)

	Stands 3A, 3B (terrace)	Stands 4A, 4B, 5 (hill slopes)	Stand 3C (lower slopes)
Group means	0.80	0.78	0.87

ANOVA tables:

1.

Source of variation	df	MS	F		F0.05
Forest Type	1	0.065	0.08 ,	P > 0.05	5.99
Microsite	6	0.850	0.81 ,	P > 0.05	2.12
Error	408	1.048			

2. ANOVA for canopy/canopy gap comparison, F=1.65, P > 0.05 (F0.05 = 3.87).

3. ANOVA for sites, F=0.28, P > 0.05 (F0.05 = 4.26).

For large miro seedlings there are no significant differences in height growth rates for seedlings growing in different forest types or on different microsites (Table 25).

TABLE 25 Height growth rates of large miro seedlings growing in different forest types and microsites, showing mean growth rates (cm/yr)

Microsite	Forest type		
	beech-podocarp	podocarp-hardwood	both types
log, under canopy	0.75	0.87	0.80
ground, under canopy	0.97	0.60	
log, canopy gap	0.94	1.17	0.89
ground, canopy gap	0.92	0.73	
Group means	0.90	0.78	

TABLE 25 (cont'd)

1.

Source of variation	df	MS	F		F 0.05
Forest type	1	0.641	0.92 ,	P>0.05	5.99
Microsite	6	0.696	0.58 ,	P>0.05	2.10
Error	168	1.206			

2. ANOVA for canopy/canopy gap comparison, F = 0.32, P>0.05 (F 0.05 = 3.89).

For large rata seedlings height growth rates are greater in beech-podocarp forest but the differences are not significant (Table 26). There are no significant differences in growth rate for seedlings growing on different sites. Seedlings growing in canopy gaps have a significantly greater mean growth rate (1.51 cm/yr) than seedlings growing under a canopy (1.18 cm/yr).

TABLE 26 Height growth rates of large rata seedlings in different forest types, microsites and sites, showing mean growth rates (cm/yr)

Microsite	Forest type		
	beech-podocarp	podocarp-hardwood	both types
log, under canopy	1.02	0.95	1.18
ground, under canopy	1.68	1.05	
log, canopy gap	1.93	1.36	1.51
ground, canopy gap	1.41	1.38	
Group means	1.48	1.19	

	Stands 3A, 3B (terrace)	Stands 4A, 4B, 5 (hill slopes)	Stand 3C (lower slopes)
Group means	1.40	1.30	1.35

TABLE 26 (cont'd)

ANOVA tables:

1.

Source of variation	df	MS	F	F 0.05
Forest type	1	9.95	1.69,	P>0.05 5.99
Microsite	6	5.88	1.92,	P>0.05 2.13
Error	408	3.063		

2. ANOVA for canopy/canopy gap comparison; F = 4.71, P< 0.05 (F 0.05 = 3.87).

3. ANOVA for site comparison; F = 0.16, P>0.05 (F 0.05 = 3.00).

For large hard beech seedlings (Table 27) there are no significant differences in height growth rate on different sites or microsites, although growth rates are higher on terrace sites (1.68 cm/yr compared with 1.19 cm/yr on hill slopes) and in canopy gaps (1.59 cm/yr compared with 1.27 cm/yr for seedlings growing under a canopy).

TABLE 27 Height growth rates of large hard beech seedlings in different microsites and sites, showing mean growth rates (cm/yr)

Microsite	Site		
	Stands 3A, 3B (terrace)	Stands 3C, 4A (hill slopes)	Both sites
log, under canopy	1.47	0.97	1.27
ground, under canopy	1.21	1.37	
log, canopy gap	1.96	1.22	1.59
ground, canopy gap	2.19	1.05	
Group means	1.68	1.19	

TABLE 27 (cont'd)

ANOVA tables:

1.

Source of variation	df	MS	F		F 0.05
Site	1	17.02	4.21,	P > 0.05	5.99
Microsite	6	4.04	1.07,	P > 0.05	2.13
Error	272	3.766			

2. ANOVA for canopy/canopy gap comparison, F = 1.58, P > 0.05 (F 0.05 = 3.88).

For large red beech seedlings (Table 28) growth rates vary significantly between the two stands where tagged seedlings were located. Both stands occupy hill slopes. Height growth rates in canopy gaps (mean of 4.63 cm/yr) are significantly greater than growth rates of seedlings growing under a canopy (mean of 2.38 cm/yr).

TABLE 28 Height growth rates of large red beech seedlings in different microsites and stands, showing mean growth rates (cm/yr)

Microsite	Stand		
	Stand 5	Stand 4B	Both Stands
log, under canopy	1.05	4.33	2.38
ground, under canopy	0.56	3.11	
log, canopy gap	3.28	5.26	4.63
ground, canopy gap	3.71	5.49	
Group means	2.31	4.68	

ANOVA tables:

1.

Source of variation	df	MS	F		F 0.05
Stand	1	180.72	6.21,	P < 0.05	5.99
Microsite	6	29.09	1.58,	P > 0.05	2.18
Error	120	18.358			

2. ANOVA for canopy/canopy gap comparison; F = 8.76, P < 0.01 (F 0.01=6.83)

A comparison of the mean height growth rates for the tagged populations of large seedlings of rimu, miro, rata, hard beech and red beech (Tables 23, 24, 25, 26, 27 and 28) with the estimated ages of seedlings of different heights, (Figs 40, 41, 42 and 43) shows that the largest seedlings must have had much faster growth rates than the mean growth rate. Thus, rimu seedlings about 100 cm tall have taken on average about 45 years to reach this height. This is equivalent to a mean growth rate of 2.22 cm/yr throughout the life of the seedling, which is much greater than the mean of 0.81 cm for the tagged sample of large seedlings (Table 23). This discrepancy in estimated growth rates is partly a result of the great variability in growth rate between individual seedlings. The maximum annual growth increments observed in the sample of tagged large seedlings (Table 29) are well in excess of the mean growth rates. A large proportion of seedlings have no annual growth in height or even sustain a decline in height through dieback or browsing (Table 30). Seedlings growing to a height of 100 cm, say, are therefore presumably seedlings with superior growth rates throughout at least part of their life span. It appears that seedlings showing negative or zero height growth over at least several years have higher rates of mortality (section 4.11.4). These seedlings are therefore less likely than seedlings with faster growth rates to attain the uppermost limit of seedling sizes.

The maximum height increments observed in tagged seedlings (Table 29) are greatest for the beech species (up to 26.5 cm increments in one year) and lowest for rimu (up to a 9 cm increment in one year). Maximum increments are, in general, proportional to the mean increments (Table 23).

TABLE 29 Maximum annual height increments among tagged large seedlings, showing individual annual height increments in cm.

Species and forest type	Stand No.						Mean (with standard deviation)
	3A	3B	3C	4A	4B	5	
Rimu: B-P	5.5	9	3	4.5	4.5	6.5	5.25 ± 1.6
P-H	5	4.5	6	5	3.5	6	
Miro: B-P	22	10.5					10.5 ± 8.2
P-H	4	5.5					

TABLE 29 (cont'd)

Species and forest type	Stand No.						Mean (with standard deviation
	3A	3B	3C	4A	4B	5	
Rata: B-P	14	10	11	15.5	9	21.5	12.5 ± 4.3
P-H	11.5	10	8	7	15	17.5	
Hard beech:	26.5	10	7.5	12.5			14.25 ± 8.5
Red beech:					26.5	18.5	22.5 ± 5.7

From paired t-test comparisons, the mean increments for rimu are significantly lower than the increments for the other species ($P < 0.05$), and other differences between species are not significant ($P > 0.05$).

B-P = beech-podocarp forest;

P-H = podocarp-hardwood forest.

A sizeable proportion of large seedlings had zero or negative height increments over the two or three year period of observation (Table 30). There are significant differences between the species.

TABLE 30 Numbers of large seedlings with zero or negative height growth increments over the two or three year period of measurement.

	No. with zero or negative growth	Total No.	%
Rimu	104	416	25.0
Miro	55	179	30.7
Rata	132	419	31.5
Hard beech	63	282	22.3
Red beech	18	131	13.7

The results of individual X^2 tests between species are summarized as follows (proportions underlined are not significantly different at the 5% level)

red beech hard beech rimu miro rata

Red beech shows the lowest proportion of suppressed seedlings (13.7%) and rata the highest proportion (31.5%). The proportions of suppressed seedlings are not directly related to the mortality rates (see Table 20); the species with the highest proportion of suppressed seedlings, rata, has the lowest mortality rate, but the species with the lowest proportion of suppressed seedlings, red beech, has one of the lowest mortality rates.

4.11.6 Population stability

An index of the stability of the small seedling populations in terms of the balance between input and output rates and the rate of turnover can be obtained from the data on establishment, density, mortality and outgrowth (sections 4.11.1, 4.11.3, 4.11.4, and 4.11.5).

A comparable analysis for large seedlings is not possible because the rate of outgrowth into the sapling size class was not determined. For populations with low large seedling densities this would be difficult to measure.

In all populations except miro, the input rate exceeds the output rate over the period of study (Table 31) indicating that the small seedling population size for all species but miro is likely to increase. Input and output rates are proportional to seedling densities, with hard beech having the highest input and output rates and miro and rata the lowest.

The rate of turnover among small seedling populations is highest for red beech and lowest for rata (Table 31). High rates of turnover indicate that establishment, mortality and outgrowth rates are high in relation to the number of seedlings in the population.

The relatively short period of observation in this study makes it difficult to predict long-term trends in population size on the basis of the measured population inputs and outputs. Periodicity in population input as a result of year to year fluctuations in seed production (see section 5.6) could mean that different input/output relationships would eventuate over a longer period.

TABLE 31 Input, output and turnover rates of small seedlings in permanent quadrats.

	Input[1] (no./m^2/yr)	Output[2] (no./m^2/yr)	Turnover[3] (%)
Rimu	0.34	0.28	43
Miro	0.02	0.06	62
Rata	0.06	0.03	17
Hard beech	2.21	1.48	54
Red beech	0.86	0.70	70

[1] Equivalent to the mean establishment rate, Table 15

[2] The sum of the mean mortality and outgrowth rates, Table 15

[3] Turnover % = $\frac{\text{mean input rate + mean output rate}}{\text{average density}} \times 100\%$

4.12 POPULATION DYNAMICS OF RIMU SAPLINGS, POLES AND CANOPY TREES

4.12.1 Rimu Saplings and poles

Saplings and poles (all individuals in the subcanopy greater than 1 m in height) are found at densities which are lower than or equivalent to the densities of canopy trees (Table 14). There is a tendency for saplings and poles to be grouped in clumps of less than five individuals, often in association with clumps of large seedlings. Saplings and poles are generally absent from the dense thickets of hardwoods in large canopy gaps and beneath the crowns of rimu canopy trees. The development sequence of rimu through the subcanopy layers is described in section 4.13.

Mortality rates are very low. Mortality among 57 subcanopy individuals in two permanent plots over a 2.3 year period amounted to one death which was equivalent to a mortality rate of 0.8% per annum (Table 32). This single death was the result of crushing by a group of adjoining windthrown hardwood trees.

Saplings and poles range in age from 25-70 years at 1 m in height (Fig.40) to 150-500 years at the time of reaching the upper canopy above the level of the hardwood (Quintinia and kamahi) canopy (Fig. 44). Most individuals reach the upper canopy in 250-400 years. The 560 year old individual (Fig.44) was in an atypical position beneath the crown of a rimu canopy tree of similar age.

The age at which individuals first reach the upper canopy is also evident in the patterns of stem diameter growth. Diameter growth accelerates markedly when trees reach the upper canopy and is sustained at a high rate for several hundred years (see Figs 35 and 47). This follows a long period of slow growth in the subcanopy when stem diameter growth is less than 0.5 mm per ring width. The ages at which the acceleration of the stem diameter growth occured in a sample of subcanopy and canopy trees are shown in Figure 45, see also Appendix VI. Most trees in the sample

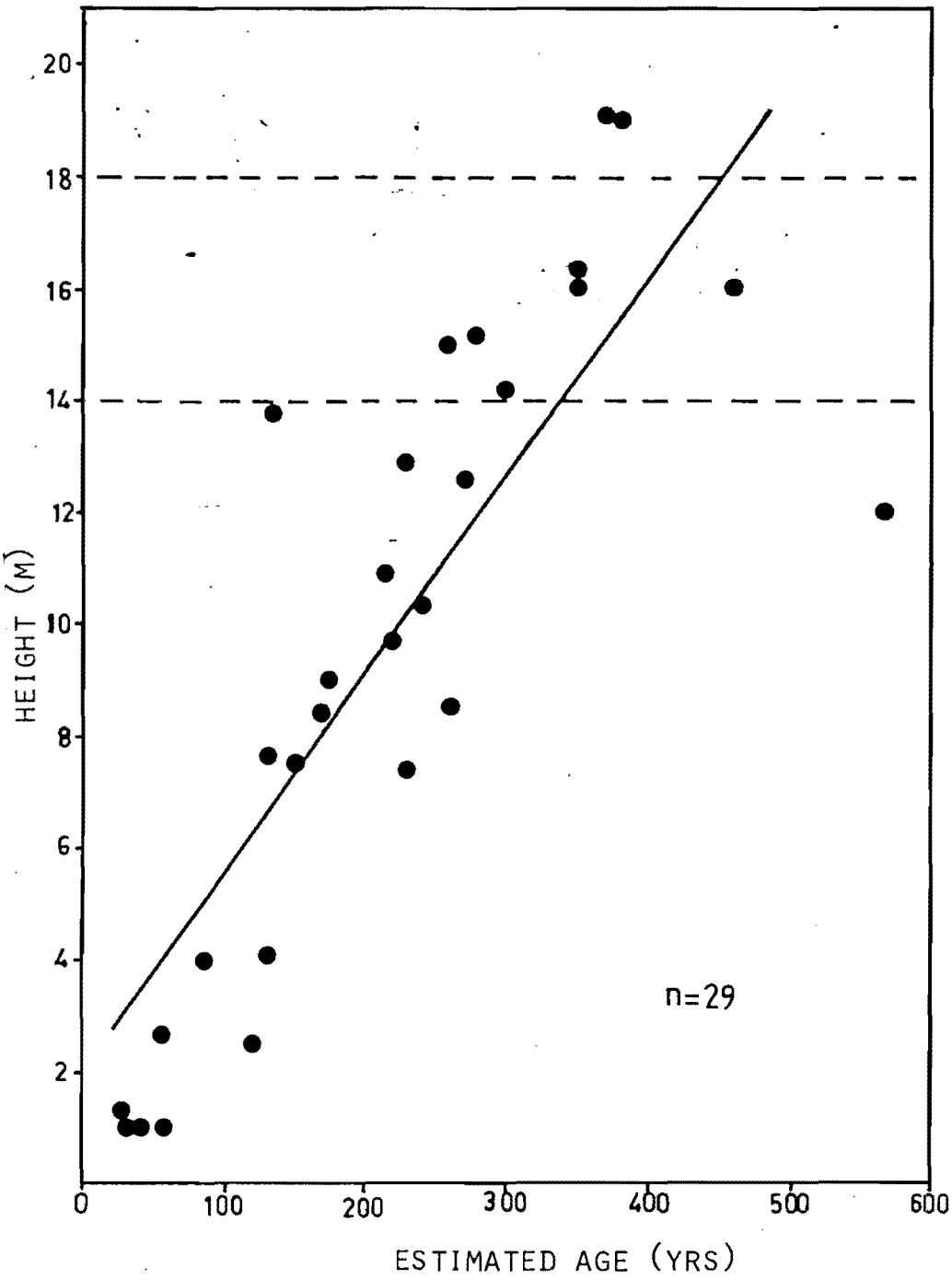


Figure 44. The age-height relationship for rimu saplings and poles in podocarp-hardwood forest. The dotted lines mark the height range of the *Quintinia*-kamahi canopy. The linear regression shown is described by $y = 0.035x + 2.01$, $r = 0.82$, $P < 0.01$.

had commenced the acceleration of growth between 100 and 200 years of age. A few canopy trees, however, showed no increase in diameter growth and these trees may have been continually suppressed by other rimu canopy trees in close proximity. In the immediately past 300 years no trees began rapid diameter growth as young as in the previous 500 year period (Fig. 45). This suggests that conditions have been less favourable for the early stages of tree growth in the past 300 years compared with those prevailing previously.

Height growth rates of saplings and poles were not measured directly. The mean growth derived from the slope of the linear regression in Figure 44 is 3.5 cm/yr. Height growth rates are much greater in individuals growing in exposed sites outside the forest. On the site of an old burn where the forest canopy had been destroyed over a large area (see Appendix V) open-grown poles had reached up to 5 m in height in the first 20 years of growth. This represents a mean height growth rate of 25 cm/yr which is seven times faster than the estimated growth rate of poles growing beneath a hardwood canopy in undisturbed forest.

4.12.2 Rimu Canopy Trees

Canopy trees are found at densities of about 20 to 60/ha in podocarp-hardwood forest and about 1 to 70/ha in Nothofagus-dominant forest (Table 14). The higher range of densities is found on lower slopes; elsewhere canopy tree densities (in podocarp-hardwood forest) are consistenly about 20/ha. Canopy trees are concentrated on ridge crests and are absent from steep-sided gullies.

Over a 2.3 year period of assessment three deaths occurred in a sample of 158 canopy trees (a mortality rate of 0.8% per annum, Table 32).

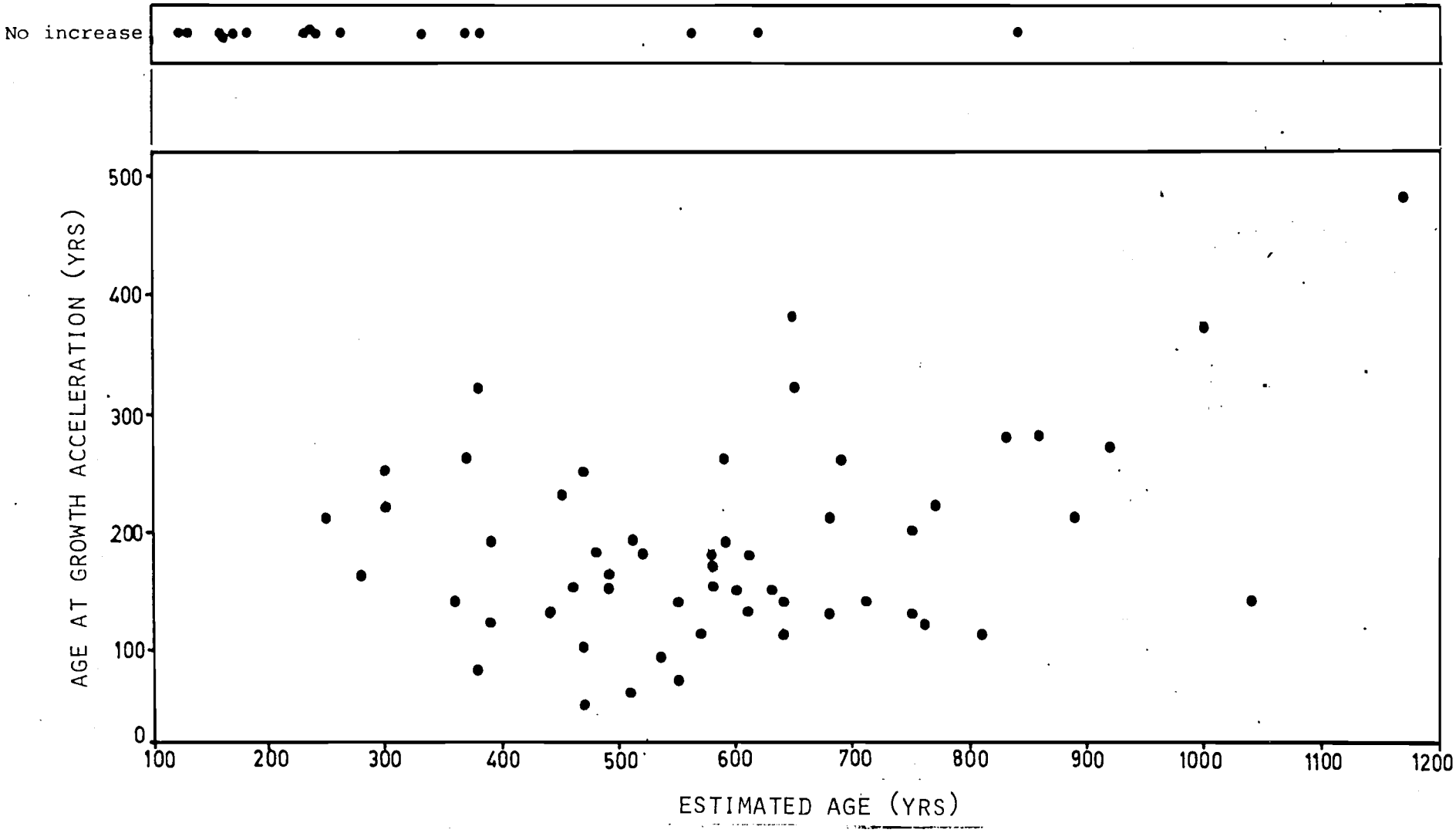


Figure 45. Age at which stem diameter growth rates in rimu increase (to a sustained rate of more than 0.5 mm per ring width). n = 74.

Table 32. Mortality rates of rimu saplings, poles and canopy trees in permanent plots.

	Stand number and period of assessment		
	Stand 1 (Oct 1975-Jan 1978)	Stand 2 (Aug 1975-Jan 1978)	Both stands (2.3 years)
Saplings and poles			
initial no.	31	26	57
no. deaths	1	0	1
% mortality p.a.	1.4%	0.0%	0.8%
Canopy trees			
initial no.	77	81	158
no. deaths	1	2	3
% mortality p.a.	0.6%	1.0%	0.8%

The second method of estimating mortality, involving a census of 494 live and 47 dead canopy trees (section 3.11), gave an estimated mortality rate of 0.2 - 0.4% per annum.

A significant proportion of canopy trees are blown over or knocked over by the falling of adjacent trees, but most trees die in situ without the cause of mortality being apparent (Table 33). A number of fungal and insect parasites of rimu trees have been documented (Franklin, 1968), but there was no evidence in the study area of pathogens, parasites or browsing animals causing tree death. Deaths of canopy trees occurred singly; there were no episodes of synchronized deaths over a wide area evident in the study area. Rimu trees were not affected by the 1970/71 summer drought which led to the widespread mortality of mature Nothofagus fusca trees on hill country sites in and beyond the study area (section 4.13.4).

Table 33. Causes of mortality in rimu canopy trees.

Cause of Mortality	Number
Undetermined:	
decayed fallen trees	19
in situ	14
Windthrown:	
uprooted	7
broken stem	7
	47

Rimu is considered to be windfirm on deep soils (Franklin, 1968). On hill slopes in the study area rimu is considerably more windfirm than the other canopy species with the exception of rata. The directions of fall of windthrown trees are shown in Figure 46. Most trees fall away from the direction of westerly winds and most of the remainder fall away from the east to south-west sector. The predominant surface wind direction, from the north-east (N.Z. Meteorological Service records for Totara Flat), does not appear to cause the windthrow of trees.

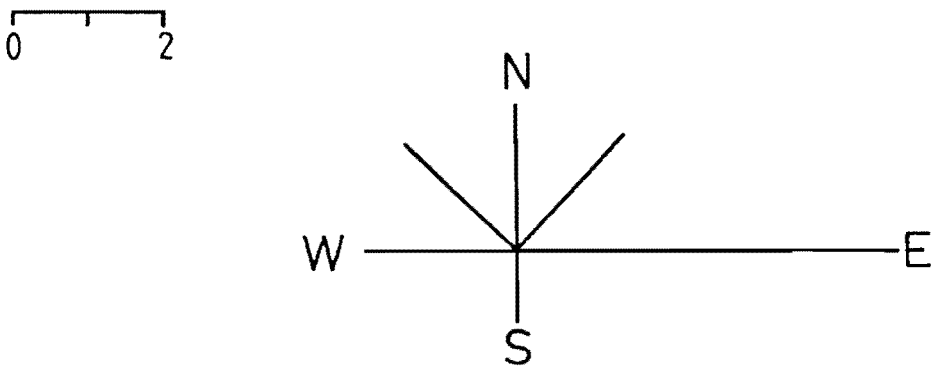


Fig. 46. Directions of fall of windthrown rimu canopy trees (n = 14).

Although the sample is small, the range and relative frequencies of windthrow directions support the observation that trees die singly in separate events rather than as a result of catastrophic events such as gales.

Tree diameter growth rates are initially slow during the period of suppressed growth in the subcanopy (Fig 35). Growth rates increase as trees emerge from the upper hardwood canopy, are maintained at relatively high levels for several hundred years and then decline. Diameter growth rates in the later stages of life can be as slow as in the suppressed subcanopy stage. The changing rates of diameter growth in two canopy trees are illustrated in Figure 47. Data for all measured sections are in Appendix VI. These examples show the considerable differences in the lengths of the early and late suppressed growth phases between individual trees.

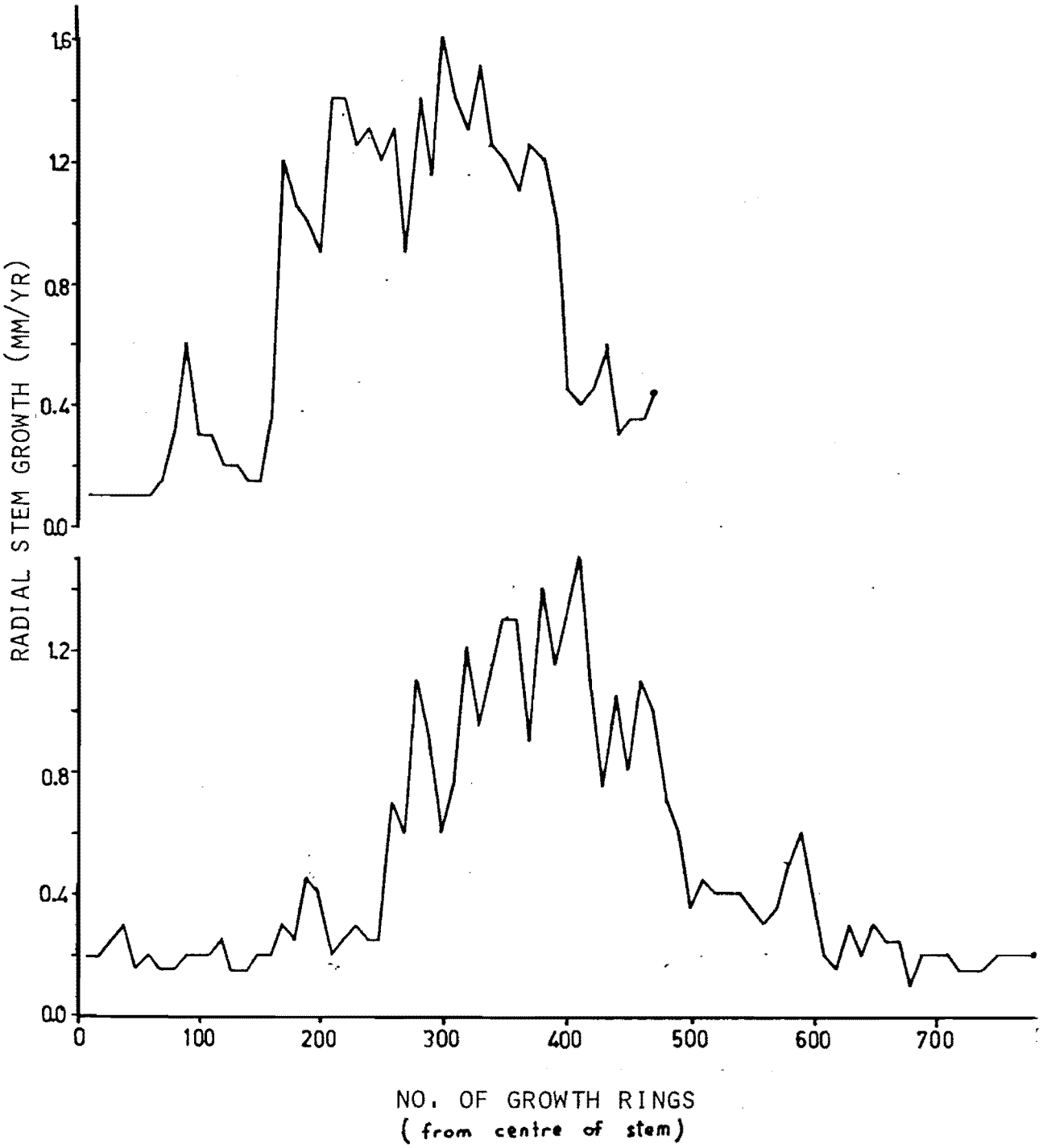


Figure 47. Diameter growth rates of two individual rimu canopy trees (estimates along a single radius). See Appendix VI for ring width data for other rimu trees.

4.13 RECRUITMENT TO THE CANOPY

4.13.1 Canopy gap formation and infilling

Canopy gaps formed by the death of single trees or groups of canopy trees are infilled by the outgrowth of branches from peripheral canopy trees and by regeneration on the forest floor within the gap. Gaps up to 300 m^2 in area can be formed by the windthrow of large trees and smaller gaps by the senescence or death of canopy trees which remain standing.

In podocarp-hardwood forest, gap colonizers are predominantly Quintinia acutifolia and Weinmannia racemosa, although Metrosideros umbellata, Phyllocladus alpinus and Coprosma foetidissima are also important colonizing species. A number of other shrub and tree species also colonise canopy gaps. These include Myrsine salicina, Coprosma australis, Elaeocarpus dentatus, Ascarina lucida and Pseudopanax simplex. In large gaps Aristotelia serrata, Carpodetus serratus and Melicytus ramiflorus may also become established. In beech-podocarp forest Nothofagus species are the predominant colonisers, although Quintinia acutifolia and Weinmannia racemosa are frequent and the other tree and scrub species occasional gap colonisers. Q.acutifolia and W. racemosa reproduce prolifically in newly-formed canopy gaps by seedling establishment, suckering and the formation of epicormic shoots on windthrown trunks. Dense thickets of hardwood saplings soon develop in canopy gaps with densities of over 100 stems/m^2. Height growth is rapid and the level of the canopy is reached in 50-70 years. During the period of gap infilling, the density of the hardwood stems steadily decreases through self-thinning and occasionally by windthrow. Initially, the hardwood sapling thickets have a strong shading effect on the ground layer but with height growth and foliage thinning, the ground layer becomes less

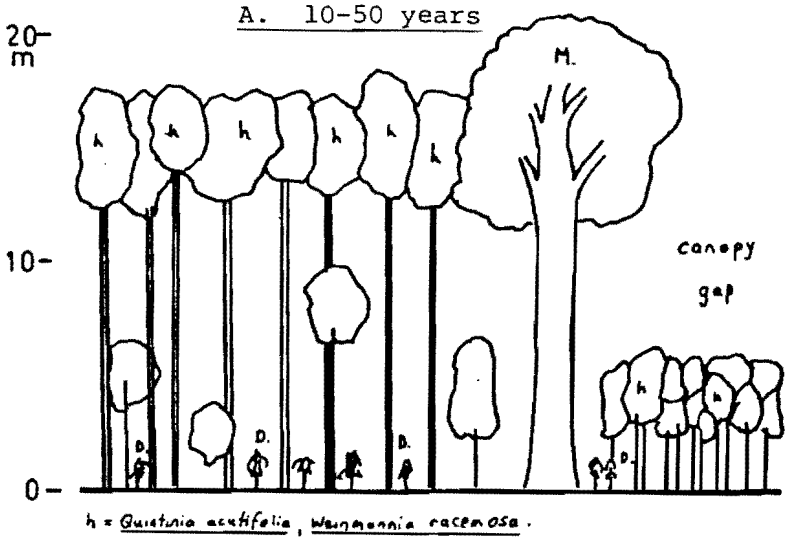
shaded and a light understorey of shrubs and ferns develops. Q. acutifolia and W. racemosa in the study stands have maximum ages of 250-300 years, and their canopy thins with advancing age.

4.13.2 Influence of canopy composition and structure on recruitment of rimu (see Fig 48)

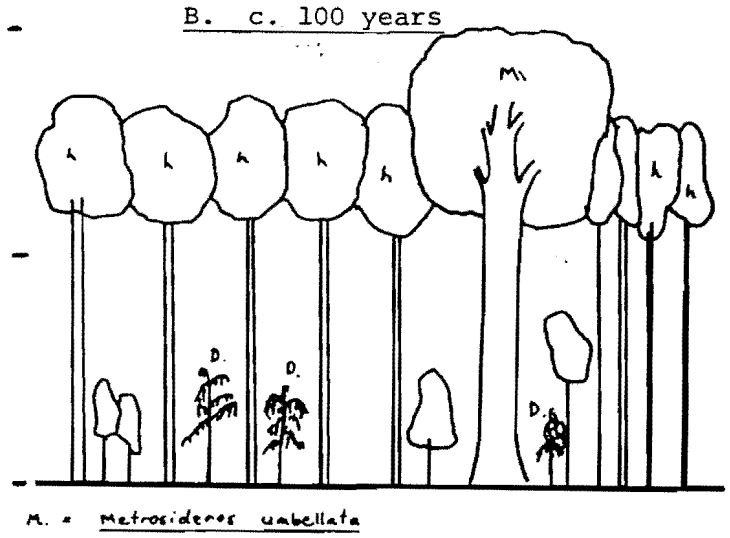
Recruitment of rimu to the canopy does not proceed directly beneath the canopy of mature rimu trees. Saml1 seedlings are found in this position but do not develop further. Rimu seedlings are absent or very infrequent beneath the dense thickets of hardwood species colonizing canopy gaps. Apart from these two unfavourable growing positions most ground space in the stand, which is occupied by mature hardwood canopy trees with an open understorey, is available for rimu recruitment.

During the period of recruitment to the canopy, rimu seedlings, saplings and poles are normally growing beneath a hardwood canopy (Table 34). There is no clear dependence on overhead gaps in the canopy for recruitment. Large seedlings, saplings and poles in a healthy condition in all stages of development are present under a continuous hardwood canopy, but do not grow through the denser hardwood foliage layers. In many situations beneath a dense overhead canopy the light regime appears to be influenced by the presence of large canopy gaps nearby. These gaps may be important for providing adequate light intensities for sapling and pole development over wide areas beneath a continuous canopy.

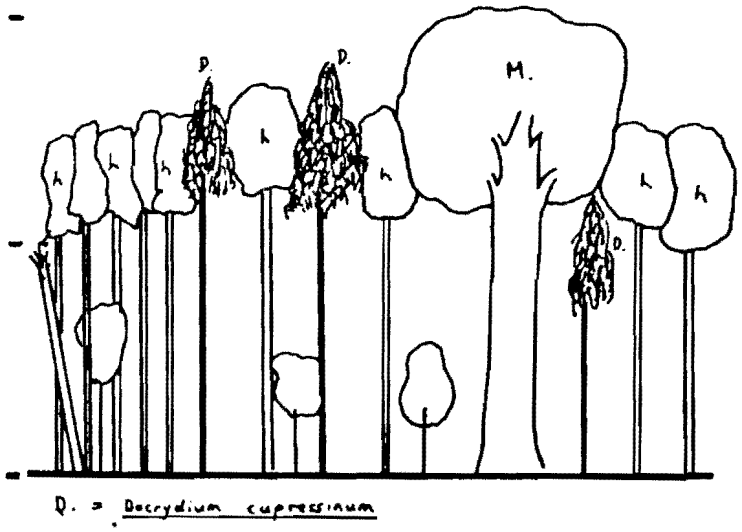
There appear to be two main growing positions for the initial development of rimu to the large seedling stage (see Table 34). Some seedlings have established under mature hardwood trees which may be up to 200 years older. The remainder have established beside hardwood trees as little as 15-20 years older, and in one case (sample number 3, Table 34) within and around a small canopy gap. These observations suggest that canopy gaps are necessary for the establishment of a significant proportion of the seedling population. For the remainder, the opening of the canopy



Seedling establishment under a continuous canopy of mature hardwoods (nearby canopy gap provides side light) and around periphery of a recently formed canopy gap



Development to pole stage under continuous hardwood canopy



Attainment of the upper canopy level by growth through an open hardwood canopy

Figure 48. Stages of recruitment to the canopy for rimu in podocarp-hardwood forests (a diagrammatic representation).

Table 34. Growing positions of large seedlings, saplings and poles of rimu in relation to stand structure.
('Hardwoods' refers to Quintinia acutifolia, Weinmannia racemosa and Metrosideros umbellata, the principal canopy species. Estimated ages are in brackets.)

Sample number	Rimu individual or group	Canopy structure
1	Pole, 11 m tall (200 yr)	Overshadowed by older hardwoods (220-250 yrs, 18 m tall). Large canopy gap 5 m away gives side light.
2	Two suppressed large seedlings (25, 32 yrs)	Overshadowed by old hardwoods (240 yr) forming a continuous canopy. Canopy gap formed by leaning M. umbellata tree 15 m away which gives side light.
3	Group of 15 large seedlings in 100 m^2 area (5-54 yrs)	Within and around small canopy gap created by two fallen hardwoods 40-54 yr ago.
4	Six large seedlings (28-46 yrs)	Under continuous hardwood canopy (100 yr). Close to a gully giving side light.
5	Pole, 8.4 m tall (170 yr)	Under large M. umbellata (230 yr). Other overshadowing hardwoods are younger than 170 yr.
6	Pole, 8.5 m tall (260 yr)	Under a dense hardwood canopy (180 yr, 270 yr) and a large Phyllocladus alpinus tree (340 yr). No canopy gaps nearby.
7	Pole, 7.4 m tall (230 yr)	Under dense hardwood canopy which includes a large M. umbellata tree (>300 yr) and younger Q. acutifolia (120 yr).
8	Sapling, 4 m tall (95 yr)	Under dense hardwood canopy including M. umbellata tree (>300 yr) and Q. acutifolia (110 yr).

in close proximity to the site of establishment rather than directly overhead may be necessary. For those seedlings which establish in canopy gaps the development of dense thickets of hardwoods largely prevents establishment in the centre of the gap, but still permits establishment around the gap margins. The reduction in root competition resulting from the death of canopy trees could also influence the establishment and development of rimu seedlings within and around canopy gaps.

Rimu seedlings establishing in newly-formed canopy gaps are unable to grow as rapidly in height as the hardwood species established at the same time. A period of 100 to 500 years is required for rimu to reach the upper canopy level (section 4.12.1) whereas Quintinia, kamahi, hard beech and red beech can reach the canopy in 50 to 70 years. Thus, rimu is unable to reach the canopy without being suppressed by competition from the faster growing hardwoods.

The diameter growth rates of rimu saplings and poles are consistently slow (less than 0.5 mm per ring width). A rapid acceleration of diameter growth coincides with the attainment of the upper canopy level above the canopies of competing hardwood trees (section 4.12.2). During the period of suppressed subcanopy growth there are occasional short periods of relatively fast diameter growth in some individuals (see Fig. 47). These short fluctuations in growth rate could be responses to openings and subsequent infillings in the surrounding canopy. As an example, the rimu pole with an estimated age of 230 years (sample number 7, Table 34) shows faster diameter growth between 50 and 110 years ago. Growing next to the pole is a hardwood tree aged 120 years. This tree presumably established in a canopy gap, the formation of which resulted in a period of rapid growth in the already established rimu pole. The period of rapid growth continued until the filling of the canopy gap about 60 years later. Growth rates of rimu saplings and poles

during the long period of recruitment to the canopy, therefore appear to be influenced by the successive formation and infilling of canopy gaps.

4.13.3 Regeneration characteristics of the major canopy tree species

Large seedlings and saplings of red beech, hard beech, rata, Quintinia and kamahi are capable of rapid height increments under conditions of adequate light in canopy gaps. Miro and rimu seedlings and saplings grow more slowly even under optimal growing conditions in the understorey (see section 4.11). Differences in seedling growth rates are shown by the average time taken for seedlings growing under a variety of canopy conditions throughout the stand to attain 1m in height (Table 35).

Relative differences in height growth rates of large seedlings are maintained throughout the period of recruitment to the canopy. Thus Quintinia, kamahi, red beech, hard beech and rata are able to rapidly occupy gaps created in the canopy by the death of existing canopy trees. These species are directly recruited to the canopy without a long period of suppression under the canopy of other trees. Rimu, miro and in some instances individuals of rata are unable to grow as rapidly as the other species in the sapling and pole stage and they are overtaken in height growth and suppressed by the other species during the process of gap replacement. The average time for each species to be recruited to the canopy ranges from 50 to 70 years for red beech, hard beech, Quintinia and kamahi and up to 250 to 400 years for rimu (Table 35). Miro appears to have a similar recruitment period as rimu, and rata a recruitment period of intermediate length (60-100 years).

The patterns of recruitment to the canopy indicate differences in the shade tolerances of saplings and poles of each species. All species appear to be dependent on canopy

Table 35 Summary of regeneration characteristics of the major canopy tree species.

Species	Seedling population size [1]	Growth rates of large seedlings (age at 1 m in brackets)	Length of recruitment period	Conditions for recruitment	Maximum life span [2]
rimu (*Dacrydium cupressinum*)	small	very slow (45 ± 25 yr)	long (250-400 yr)	continuous canopy with small overhead gaps or large gaps nearby	long
rata (*Metrosideros umbellata*)	small	moderate (25 ± 10 yr)	medium (60-100 yr)	large and small canopy gaps	long
miro (*Podocarpus ferrugineus*)	medium	slow (35 ± 5 yr)	long	continuous canopy with small overhead gaps or large gaps nearby	long(?)
red beech (*Nothofagus fusca*)	medium	rapid (15 ± 15 yr)	short (50 - 70 yr)	large canopy gaps	medium
hard beech (*N. truncata*)	large	moderate (25 ± 10 yr)	short (50 - 70 yr)	large and small canopy gaps	medium
Quintinia acutifolia	large	rapid	short (50 - 60 yr)	large canopy gaps	medium
kamahi (*Weinmannia racemosa*)	large	rapid	short (50 - 60 yr)	large and small canopy gaps	medium

[1] See Table 14 for quantitative data.

[2] Long - greater than 600 years.
Medium - approx. 250 to 300 years.

openings to varying degrees, although miro and rimu are able to survive long periods of suppression under a continuous overhead canopy. The shade tolerances of the seven species, based on observations of the growing positions and growth rates of the sapling and pole stage, are in order of decreasing tolerance: miro > rimu > rata > hard beech and kamahi > red beech and Quintinia. Only miro and rimu appear to be able to survive a period of continuous suppression with slow or interrupted height and diameter growth in the subcanopy (see section 4.12.1 for the growth rates of suppressed rimu individuals), but the remiander of the species can tolerate suppressed growth for short periods during recruitment. The canopy conditions under which recruitment for each species normally occurs are summarised in Table 35.

4.13.4 The role of catastrophe in regeneration

The hill country podocarp-hardwood forests in the study area do not appear to be subject to large-scale natural disturbance from gales, fire, landslips or drought. The beech-podocarp forests are more subject to disturbance because of the greater susceptibility of the Nothofagus species to windthrow on ridge crests and to drought and associated pathogen attack. Hard beech dominant hill country stands in the study area are prone to windthrow from south-easterly gales. Stands on ridge tops and exposed upper slopes can be extensively windthrown at infrequent intervals of 50 years or more. This is particularly evident in Granvill State Forest and the Flagstaff area of Hochstetter State Forest where there are extensive beech pole stands containing remains of windthrown trees. Red beech is apparently drought prone on some hill slopesites in the study area. Widespread mortality followed the 1970/71 summer drought (C.D. Gleason, pers comm, 1975) and resulted in the death of a high proportio of canopy trees in Stand 4 (Fig 33) and adjoining areas of

Granville State Forest. Red beech stands on hill slopes in nearby Stand 5 (Hochstetter State Forest) were largely unaffected). Mortality of large red beech trees in other areas of north Westland was observed following a period of below average rainfall in 1970/72 and again in the Maruia district in 1977/78 (Kershaw, 1980). Outbreaks of the defoliating insect Inglisia fagi were also implicated in the tree deaths.

Widespread mortality of red beech and other beech species during the 1971-72 period has been observed in other regions of the South Island (Burrows and Greenland, 1979). The large sizes of the trees killed in Stand 4 (estimated to be up to 300 years old) indicate the rarity of catastrophic events of this nature. The beech species in north Westland and elsewhere are also prone to occasional episodes of large-scale mortality following insect pathogen attack (Conway, 1949; Rawlings, 1953; Milligan, 1972). This mortality may be associated with physiological stress caused by droughts for example.

Quintinia and kamahi are also susceptible to windthrow, but small groups of trees rather than large areas of the canopy are generally affected.

Rata, miro and rimu are, by comparison, windfirm on hill slopes and do not appear to be affected so severely by pathogen attack or climatic stress.

Red beech and hard beech respond to catastrophe-induced canopy destruction by rapid and prolific regeneration involving new seedling establishment and the large populations of existing seedlings. Dense to moderately dense stands of saplings and poles develop as a result. In podocarp-hardwood stands subject to large-scale windthrow, Quintinia, kamahi and to a lesser extent rata respond to the canopy destruction by abundant regeneration. Rata has the ability to form epicormic shoots from leaning and fallen large stems (Veblen and Stewart, 1980) and this habit may have, in the past,

produced the small groups of canopy tree stems found in the study area. Rimu and miro regeneration is not stimulated by the catastrophic opening of the canopy because of the subsequent dense regrowth of the hardwood species.

In the absence of prolific regrowth of the beech species, Quintinia and kamahi, rimu and to a lesser extent rata and miro are able to colonize readily and form dense stands of saplings and poles in places. This can occur where human activity has resulted in massive disturbance or destruction of the forest canopy. An example is found along a ridge near Stand 2 where repeated burning within the past 100 years has resulted in a low shrub vegetation dominated in places by rimu saplings and poles. The vegetation composition and location of this area is described in Appendix V. Adjoining ridges, which were presumably not subjected to repeated burning, are covered with dense pole stands of Quintinia and kamahi with some rata beneath which there are occasional, suppressed seedlings and saplings of rimu. The rapid and prolific recovery of the hardwood species in this case has inhibited the regeneration of rimu. This response would be expected to follow natural catastrophes since these are unlikely to result in the complete elimination of the hardwood species (Fire does not occur naturally in the forests of the study area). Natural catastrophes which destroy the existing mature stands over extensive areas are therefore unlikely to result in more abundant rimu regeneration than the normal processes of canopy gap formation in otherwise undisturbed stands. In stands affected by logging activity, the frequency of rimu seedlings establishing or developing after logging is, in general, about the same as in undisturbed forest on the same sites. Seedlings are accordingly more common on poorly-drained terraces compared with hill slopes.

An exception occurs in silver pine - rimu terrace stands where all merchantable rimu trees have been removed (Hughes, 1975). Rimu seedlings are infrequent and do not increase in frequency for at least 30-40 years following logging.

CHAPTER FIVE
DISCUSSION

5.1 STABILITY OF THE BEECH FOREST BOUNDARY

Nature of the boundary

The boundary between beech forest and adjoining forest or scrubland communities is in general sharply defined with a nearly continuous beech canopy up to the boundary (section 4.4). Given the gregarious nature of the Nothofagus species and a mode of migration predominantly involving the marginal expansion of stands, this pattern is consistent with an advancing boundary. It does not indicate retreating or static distribution limits where the boundary between Nothofagus dominant and adjoining communities would be indistinct with many small stands and individuals occupying favourable sites away from the boundary. Indistinct boundaries and distribution patterns consistent with a static boundary are found along the lower altitudinal limits of the N. menziesii zone in the southern Paparoa Range and in the coastal area between Rapahoe and Barrytown.

Boundary age profiles

The age structures of the Nothofagus populations along the beech forest boundary in the study area are generally characteristic of an advancing boundary; canopy gaps in the forest communities adjacent to the boundary are usually occupied by Nothofagus seedlings, and the canopy trees forming the boundary generally belong to the younger age classes (section 4.4). It is very uncommon to find old canopy trees or large dead trees in the absence of seedlings forming the boundary, which would be the pattern with a retreating boundary. These observations apply to the main beech forest front, to the margins of the podocarp-hardwood forest enclaves and to the outlier stands. Exceptions are found along the lower boundaries of N. menziesii in the southern Paparoa Range where older trees are more common

at the boundary and near the coastline. Outside the study area there is evidence for a static or retreating boundary in the Punakaiki area and the Taramakau Valley (section 4.3).

The age profiles across sampled sections of the boundary (section 4.7) show that the advancement of the boundary must have continued at least since the date of establishment of the oldest trees near the boundary 350 years ago.

The position of the beech forest boundary

The position of the beech forest boundary in north Westland cannot be correlated with the known regional patterns of variation of soils or climate, although there is some evidence that the boundary is associated with a regional floristic boundary (section 4.8). On a local level the boundary is not limited to particular sites but crosses site boundaries in many places.

There appear to be no climatic, soil or site barriers to a further southward extension of range. The central area of Westland has a similar range of soils and local climates to the remainder of the region where Nothofagus is present. In north and south Westland the four Nothofagus species, either singly or in combination, are able between them to occupy most growing sites from sea level to timberline. The Nothofagus range extends into Canterbury, Fiordland and north-west Nelson (Fig. 2) where an even wider range of climatic and site conditions is encountered.

In South Westland an expansion of the Nothofagus range is evident in the species distribution patterns and the nature of the present-day boundaries (Holloway, 1954; Wardle, 1980a, 1980b). Three of the species have a relict distribution of small, scattered stands in some parts of the region, however; N. fusca in the forests to the south of the Arawata River (Holloway, 1954), N. solandri

var cliffortioides in the Paringa district (Wardle, 1980a) and N. truncata in the Jackson's Bay district (June, 1977).

In view of the wide ecological amplitudes and strong competitive abilities of the Nothofagus species in Westland and the apparent lack of climatic or site barriers, the further southward spread of Nothofagus into central Westland can be expected.

5.2 THE MIGRATION OF NOTHOFAGUS

The poor dispersal ability of the Nothofagus species compared with other tree species has been commented on by many observers (see Darlington, 1965). This study provides further evidence regarding the dispersa ability of the New Zealand species.

Migration occurs in two ways; by slow marginal spread or by the more rapid long distance dispersal. Long distance dispersal over distances of up to 12 km has apparently occurred in the study area (section 5.3), but events of this nature would be rare or infrequent, particularly more than several hundred metres from the parent boundaries and in the lowland forests. The likely contribution of long distance dispersal to the overall rate of migration varies throughout the study area. In the upland zone of the southern Paparoa Range long distance establishment is more frequent than in the lowland forests, and the outliers potentially contribute 54% of the expansio of range by marginal spread. In the lowland forests the potential contribution to expansion is smaller (20%) but still important (section 4.7).

The estimated rate of migration by marginal spread, about 0.1m/year (section 4.7; Wardle, 1980a), is extremely slow compared with migration rates derived for large-seeded northern Hemisphere species. Post-glacial migration rates in the order of 100 to 300 m/yr for Quercus, Fagus, Castanea and Picea spp. have been derived from the fossil record at widely spaced localities (Davis, 1976; Hoeg, 1978). There is at least one tree species for which rates of migration similar to those of Nothofagus have been estimated Mora excelsa in Trinidad (Beard, 1946). This species has a large fruit which is not apparently dispersed by animals.

Nothofagus migration rates do not appear to have been estimated in other countries. The expansion of Nothofagus range by marginal spread and the formation of outliers is evident in parts of Victoria and New South Wales Australia (Fraser and Vickery, 1938; Howard and Ashton, 197 but in other places Nothofagus shows no tendency to spread, for example, in the New Guinea Highlands (Walker, 1966).

Three factors which influence the range and rate of Nothofagus migration can be identified. These are discussed in turn.

5.2.1 Seed dispersal

The nuts of Nothofagus are winged and range from 3 to 10mm in length and from 2 to 15 mg in weight (Preest, 1963). On the basis of nut size, the species form two groups: (1) N. fusca and N. truncata with larger and heavier nuts, and (2) N. menziesii and N. solandri var. cliffortioides with smaller and lighter nuts.

Nothofagus nuts although relatively heavy, are adapted for wind dispersal by the possession of small wings. Most nuts fall beneath or close to the canopy of the parent tree. Some are carried further by wind but normally fall within 200 m of the seed source (Bunn, 1965; Wardle, 1970b). There is indirect evidence for occasional dispersal of seed over longer distances, for example, N. fusca seedlings 6 km distant from parent trees, and an adult N. fusca tree 4 km distant from the nearest seed source (C.J. Burrows, pers.comm.) at Cass and small, isolated stands several to many kilometres distant from the main beech forest area in the Taramakau catchment (Burrows, 1977). Further examples of this phenomenon in the study area are described in section 4.5

The ability of winds to carry heavy seeds and other plant material has been demonstrated at Cass where

leaves and twigs of Nothofagus are commonly found many kilometres from likely parent trees (Burrows, 1977).

Carriage of Nothofagus seed by streams and rivers has been suggested as an important dispersal mechanism (Holloway, 1954; Wardle 1970b). There are limitations to this mode of dispersal. Viable seed does not remain afloat for long (Preest, 1963) and water-borne seed would need high flood conditions to be deposited on sites suitable for seedling establishment on stream and river banks. The observed extension of the beech forest boundary along watercourses both upstream and downstream of the main area of distribution (section 4.2) suggests that the availability of favourable colonisation sites in valleys, as well as the water dispersal of seed, permits rapid migration along watercourses.

Unlike podocarp seeds which are attached to succulent scales or arils, the seeds of Nothofagus do not have adaptations for dispersal by animals. Although the seed is eaten by birds (Riney et al, 1959), introduced rodents (Campbell, 1978) and possibly wetas, it has a thin testa and is unlikely to survive passage through the gut of animals (Preest, 1963). Collection and caching of the nuts by animals, which would be a means of effecting dispersal, have not been observed. This mode of dispersal has been described in heavy-seeded species including the related Fagus sylvatica (Ridley, 1930; Grime, 1979). Caching of podocarp seeds by rats has been observed (Herbert, 1978).

5.2.2. The role of mycorrhizae in migration

The New Zealand Nothofagus species are ectomycorrhizal (Morrison, 1956; Arnold, 1959; Baylis, 1960; Mejstrik, 1972). The results of some experiments which have been conducted on the role of the mycorrihizae in Nothofagus seedling growth demonstrate a dependence on

mycorrhizal fungi from beech forest soils for continued seedling growth. N. menziesii seedlings raised in steamed podocarp forest soil ceased growth before attaining a dry weight of 50 mg whereas seedlings raised in untreated beech forest soil continued growth to a dry weight of about 500 mg by the end of the first growing season, provided that mycorrhizal associations were quickly established (Baylis, 1980). Morrison (1956) also found that mycorrhizal associations did not form in N. menziesii seedlings grown in podocarp forest soils, although mycorrhizae did develop in a pasture and a tussock-grassland soil where Nothofagus was absent at least in the recent past. N. solandri seedlings grown in high altitude field plots did not develop normally until mycorrhizae were introduced via forest litter (Wardle, 1971a). Wardle (1980a) found that N.menziesii seedlings and a N. fusca seedling growing on gravel stream fans well beyond the rooting zones of mature trees were mycorrhizal. In South America, the ectotrophic - forming fungi were absent in a burnt area previously supporting Nothofagus forest, but were present in Nothofagus seedlings which established from wind-blown seed subsequent to the fire (Singer, 1969).

Baylis (1980) has suggested that natural soils outside the Nothofagus range are unlikely to contain the appropriate fungi for Nothofagus mycorrhizae because most New Zealand species have endomycorrhizal rather than ectomycorrhizal symbionts. Leptospermum is the only other widespread New Zealand genus that can be ectomycorrhizal (Baylis, 1971) and it is possible that its mycorrhizal fungi could also form effective mycorrhizal associations in Nothofagus (Baylis, 1980). This possible role of Leptospermum in the establishment of an effective mycorrhizal association could explain the apparent rapid migration of Nothofagus across outwash terraces in the study area where Leptospermum occurs (section 4.2) and into

Leptospermum scrubland (Elder, 1941; Wardle, 1970b), and the rise in Nothofagus frequencies at the north westland sites during the early post-glacial when Leptospermum was relatively abundant (Moar, 1971).

The unthriftiness and low degree of mycorrhizal infection of Nothofagus seedlings arising from seed experimentally sown beyond the rooting zone of parent trees in this study indicate that the formation of an effective mycorrhizal association may be slow or non-existent when seed is dispersed over long distances away from a Nothofagus stand. Seedlings lacking the normal mycorrhizal association are unlikely to survive unless established on soils of high phosphorus status where the mycorrhizal symbiont is not essential for adequate nutrition (Harley, 1969; Baylis, 1980).

The requirement of Nothofagus for mycorrhizal symbionts would have the effect of limiting the rate at which the genus can spread into new habitats. Seedlings arising from the long distance dispersal of seed, unable to form appropriate mycorrhizal associations, are unlikely to give rise to new colonies of beech forest. However, the presence of mycorrhizae in the infrequent stands establishe in this way in north Westland and elsewhere indicates that the establishment of mycorrhizal associations following lon distance seed dispersal can take place. The formation of these outlier stands may be dependent on the colonisation o favourable growing sites such as recent soils of high phosphorus status with the establishment of the mycorrhizal association occurring later.

In contrast to the long distance mode of dispers the slow, marginal spread from the existing forest edge ensures the continuation of the mycorrhizal symbiosis through root contact between the parent tree and newly established seedlings. Thus, the predominant mode of migration of Nothofagus is consistent with a limitation

imposed by a requirement for mycorrhizal symbionts in soils of low fertility.

5.2.3. Availability of colonisation sites

Migration proceeds following seed dispersal by the colonisation of canopy gaps in tall forest, of low open-canopied vegetation and of bare sites such as slips. The availability of openings as sites for seedling establishment and development in the vegetation being invaded is therefore an important factor influencing the rate of migration. The importance of openings is indicated by the difference between potential and observed rates of marginal spread (when potential rates are based on observed ages of earliest seed bearing and dispersal distances, section 4.7). Potential rates of spread are twice the observed rates.

There is little evidence in the present day forests of widespread, natural destruction of the forest canopy which would facilitate migration. Large-scale windthrow occurs only in exposed sites of relatively limited area (for example in the Flagstaff area), landslides are infrequent and confined to gullies and there is no evidence of natural fires. Most disturbance of the forest canopy is caused by windthrow, snow damage, drought and pathogen attack. This involves damage to, or the death of, scattered single trees or small groups of trees and creates only limited openings for colonisation.

The considerable disturbance of the vegetation caused by human activity within this century would seem to have created many new opportunities for the spread of Nothofagus. The evidence of outlier distribution in the present day forests (sections 4.5 and 4.6.3) shows, however, that outlier establishment on sites disturbed by man's activities is very localised and, in the lowland forests, very infrequent. This suggests that large-scale disturbance of

the vegetation does not necessarily lead to a large expansion of the Nothofagus range.

Migration appears to be more rapid where the vegetation being invaded is open-canopied or of low stature. This situation is found in the southern Paparoa Range where there is frequent formation of N. menziesii outliers in tussock grassland or subalpine scrubland (section 4.2), in the Karangarua Valley where N. menziesii has invaded open heathland (Wardle, 1980b) and to a limited extent, on old burn sites in the southern Tararua Range which N. menziesii has invaded sporadically (Reid, 1948; McQueen, 1951). In parts of Canterbury, N. solandri seedlings are present up to 500m from parent trees in Leptospermum scrubland (Wardle, 1970b; Burrows, 1977). A similar situation is described for modified areas of the Kaweka Range (Elder, 1941).

In the study area the rate of migration by marginal spread appears to be slowest on hill slopes and more rapid on poorly-drained terraces and on flood plains. Downstream migration along flood plains is more rapid than upstream migration, presumably because of the long-distance dispersal of water-borne seed during flooding.

Migration rates on favourable sites such as valley floors are many times faster than the maximum potential migration rates previously calculated using data of earliest seed-bearing ages and observed dispersal distances from hill sites. There are a number of factors which could allow faster migration than expected. In some cases the valley fingers and other protuberances of the boundary could have resulted from the merging of outliers with the main boundary. This would lead to a more rapid expansion of the boundary than is possible by marginal spread from the main boundary alone. Favourable sites for migration include alluvial river terraces, stream banks and poorly-drained sections of high level terraces. These sites have

in common a vegetation with a relatively open structure : stunted forest in the case of the high terraces and new surfaces exposed by flood action and side-lit stream banks in the case of the alluvial sites. In these sites the resistance of the vegetation to invasion by the light-demanding Nothofagus species would be lower than in tall, closed forest or scrubland.

A further factor may facilitate the rate of migration on to freshly-exposed surfaces. Where soil fertility is high, as on these surfaces, beech seedling establishment could be successful without the need for appropriate mychorrizal symbionts obtained through contact with the rhizosphere of parent trees (section 4.6).

5.3 ORIGINS OF NOTHOFAGUS OUTLIERS

Outliers of the main area of distribution can arise in two ways:

(i) by establishment from seed dispersed away from existing stands, or

(ii) as relict stands remaining after a contraction in the former range.

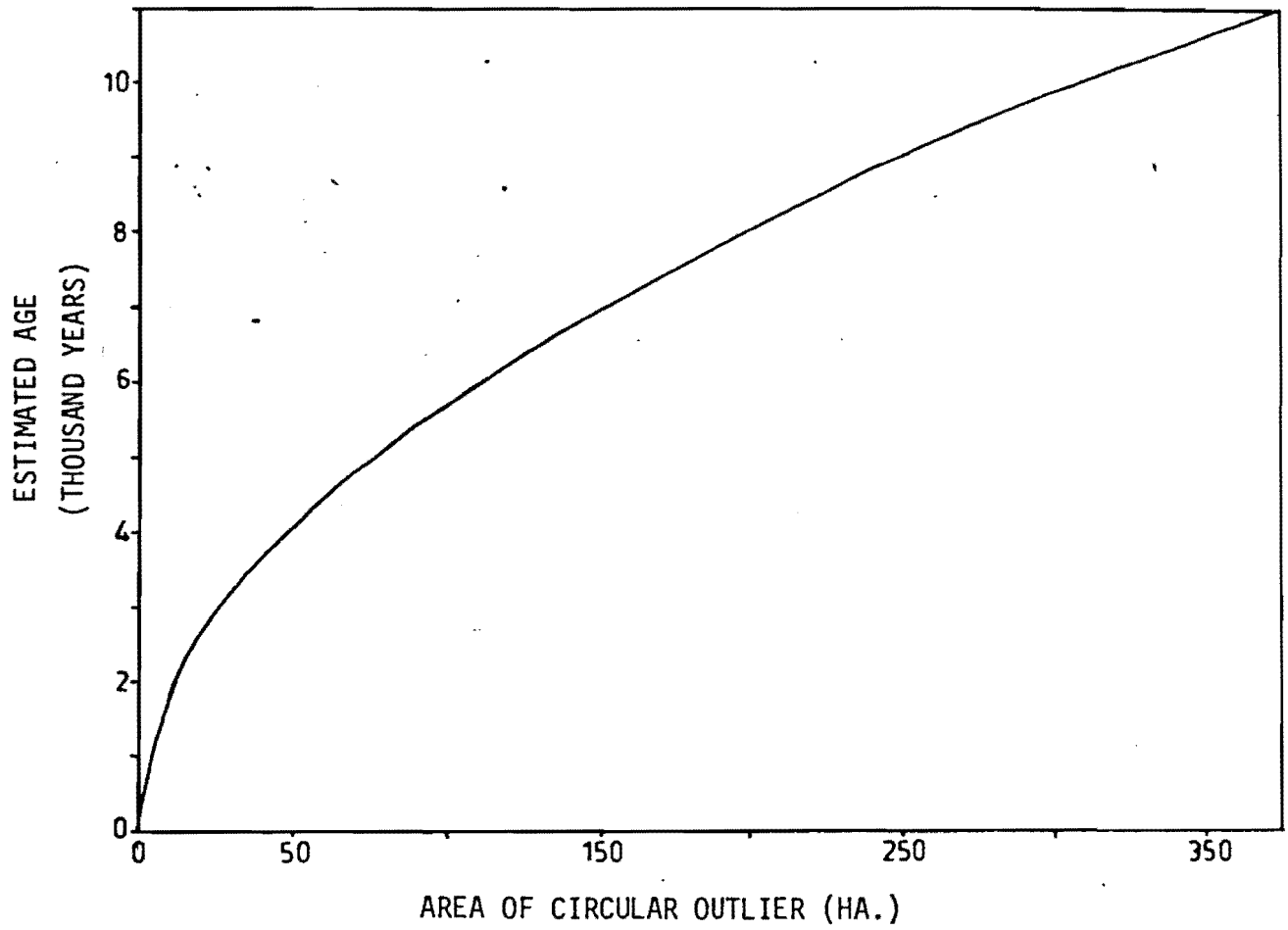
Evidence for the origins of the outliers can be obtained from the dispersion patterns and species composition of the outliers (section 4.5) and the geological history of the site occupied (see section 5.5). Dispersal of seed more than 20 m beyond the canopy of parent trees seems to be a rare or infrequent event (section 4.6) and it would be expected on the basis of the dispersal characteristics of wind-dispersed seed that the frequency of successful establishment following seed dispersal would decline at increasing distances from parent stands (Harper, 1977). Relict stands, on the other hand, would be expected to show a scattered dispersion, not related to the position of the main area of distribution. Relict stands would tend to be confined to, or centred on, favourable growing sites such as unstable gully sides in the case of Nothofagus fusca or ridge crests in the case of N. truncata. Relict outliers are more likely to be multi-species stands (depending on the range of growing sites present) whereas outliers arising from seed dispersal are expected to be single-species stands in view of the low probability of dispersal events.

Most outliers are located close to the presumed parent boundary and the frequency of outliers within 4-5 km of the parent stand declines exponentially with increasing distance from the parent stand (Fig 17). These outliers are mostly single-species stands. These features are consistent with a seed dispersal origin, the seed being derived from the stationary or slowly expanding boundaries of the main area of distribution. The frequency distribution of distances of outliers from parent stands (Fig 17) indicates that there are more outliers further than 4-5 km from parent stands than expected on the basis of the relationship for outliers closer to the parent stands. These more distant outliers could be of relict origin, or could represent unusually favourable localities for long-distance seed dispersal and outlier establishment. This group of 11 outliers are all located in the

Moana-Bell Hill district (section 4.2.8) with the exception of the Blackwater Creek outlier. The smaller stands in this group occupy a wide range of growing sites and do not therefore appear to represent one particular type of site especially favourable for establishment.

The change in slope in the size-frequency distribution of outliers (Fig 15) could represent different origins and survivorship for stands smaller or larger than about two hectares, with the smaller stands having a high chance of disappearance by merging with other beech forest because of their proximity to parent stands, and the larger stands representing expanding, long-established outliers which may be of relict origin. An alternative explanation is that the rate of formation of outliers may have increased at some time in the recent past. This latter interpretation would require the assumption that outliers expand at a constant rate from the time of establishment, i.e. that outlier size is proportional to its age. The relationship between outlier size and age based on this assumption and using the calculated mean rate of marginal spread on hill slopes (section 4.7) is shown in Fig 25. Estimates made in this way suggest the date at which the rate of outlier formation may have increased to be about 600–860 years ago (for outlier sizes of between one and two hectares). The faster migration likely on other sites would place this postulated event in a more recent period.

Mixed species stands are more frequent than expected on the basis of the species arriving independently (Table 11). This feature would be consistent with a relict origin. Alternatively, the outliers could have originated on particularly favourable sites for establishment, or the presence of one species as an outlier could have created conditions favourable for the establishment of another beech species. The first of these two alternatives is unlikely to apply to all outliers because of occurrence of multiple-species outliers on a range of growing sites which include sites normally supporting a closed tall vegetation with few opportunities for invasion, and the availability of other similar unoccupied sites in the general area. The second explanation could reflect the importance of mycorrhizae in effecting seedling establishment beyond the



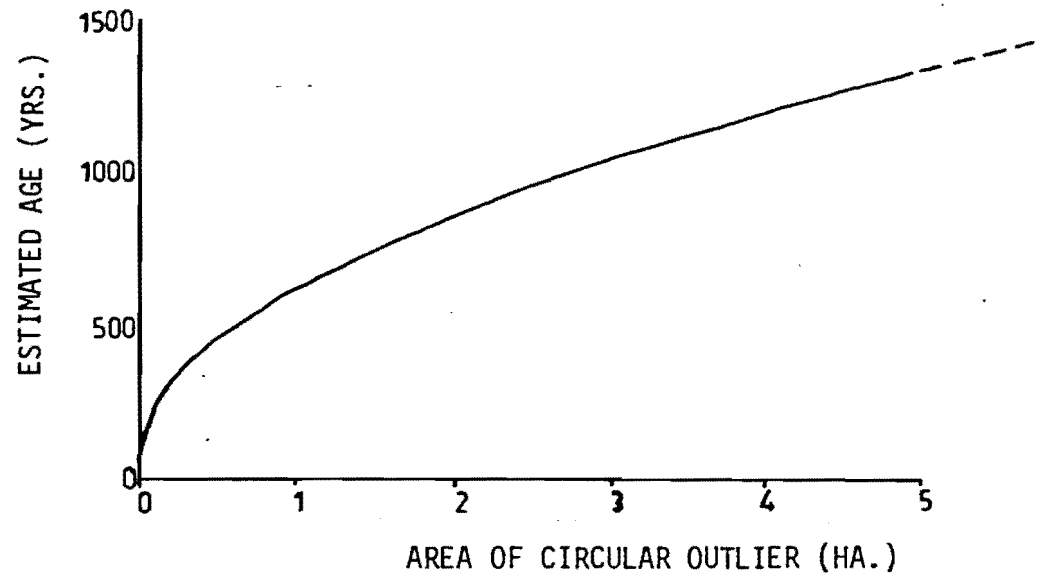


Figure 25. Hypothetical relationship between the area of a circular outlier and its estimated age.

(assuming a constant rate of expansion of 0.1 m/yr in radius along the perimeter, and a first generation time of 60 years).

rhizosphere of existing stands (section 5.2.2). One species could act as a primary coloniser of relatively fertile sites such as slips, thereby avoiding the need for mycorrhizal associations. Subsequent to the initial colonisation the dispersal of appropriate mycorrhizal fungi could be effected and the establishment of other species arriving at the site would thereby be enhanced. In the lowland forests N. fusca would be likely to act as the primary coloniser in view of its predominance at the present day beech forest boundaries and in outliers.

The number of species in lowland outliers appears to be related to the size of the stand and not to the distance of the outlier from its presumed parent stand (section 4.5). The larger the outlier, the more species are likely to be found in it. Since the larger an outlier is, the older it can be presumed to be, it follows that the larger it is, the longer is the period it has been available for colonisation by a second species of Nothofagus. This means that the number of species in an outlier cannot be simply interpreted as evidence for either a relict or a long distance dispersal origin without reference to the outlier's size.

The lack of a direct relationship between the number of species in an outlier and its distance from parent stands does not follow the pattern expected with independent long distance dispersal in which the frequency of multiple species stands should steadily decline with increasing distance. If anything, the opposite trend occurs which would indicate a relict origin or particularly favourable outlier locations, as suggested previously.

The plot of outlier size versus distance from presumed parent stand (Fig 19) emphasises the atypical characteristics of particular stands. The group of stands more distant than 5 km has already been referred to. Of this group the large Blackwater Creek outlier is separate from the remainder because of its size. Its likely origin, together with the likely origin of the large Deep Creek outlier and the moderately large Orangipuku River outlier are discussed below. The four large upland outliers in the southern Paparoa Range close to the main boundary form a separate group on the plot. These are nearly contiguous with beech forest immediately to the west across the narrow tussock grassland zone on the main dividing ridge (Figs 8 and 9).

These stands have presumably originated from seed dispersed the short distance over the dividing ridge from the west, which forms a barrier of 90–150 m in altitude and 300–600 m in width. Without this barrier which is above the beech timberline, these outliers would have joined with the main boundary. Their continued existence depends on the position of the barrier.

The fossil record points to a major contraction in Nothofagus range during the Otira Glaciation but not at any time following the reestablishment of a forest cover in north Westland at about 10 000 years B.P. (see section 5.5). Outliers at some distance from the present main beech forest boundary and originating as relict stands are therefore likely to date from the Otiran – early Aranuian period.

Some outliers, including those at long distances from the main boundary, are found in areas which were covered by the Otiran ice advances (see Suggate, 1965). These include the outliers along the Orangipuku and Crooked Rivers and at Lady and Kangaroo Lakes. This means that such outliers are likely to have established in the post-glacial period by means of long distance seed dispersal over distances of at least 12 km. The Orangipuku River outlier is on an earlier, alternative course of the Taramakau River. Water-dispersed seed from the upper Taramakau catchment where the two species forming the outlier (N. fusca and N. menziesii) are widespread could have given rise to the outlier. For the other outliers, dispersal of seed by wind across land would be necessary for their establishment.

The large size of the Deep Creek outlier may be in part a result of rapid migration along the flood plain of Deep Creek. Most of the outlier occupies this site (see Fig 13). Three Nothofagus species are present but the small size of the N. menziesii outlier (0.1 ha) and its position on a favourable growing site suggests a recent arrival for this species. (A dispersal distance of 12.2 km from the nearest boundary of the main area of N. menziesii would be involved). The outwash gravels occupied by the southern margins of the outlier are of the Loopline Formation (Gregg, 1964) which is correlated with the $K2_2$ advance of the late Otira Glacial (Suggate and Moar, 1970). The ice limit of the $K2_2$ advance came within several kilometres of the eastern end of the outlier and covered its western end. The K3 advance ice limit was even further to the south

but ice from earlier advances ($K2_1$ and K1) would have covered the site (Suggate, 1965). The three-species composition and large size of the outlier would be consistent with a glacial relict origin. However, these features appear to be a consequence of comparatively recent, long distance dispersal for at least one species (N. menziesii) and with rapid spread in a favourable site for the other two. The location of the outlier in relation to the ice limits of the Otiran glacier advances is an unlikely position for a forest refuguim and an origin from post-glacial long-distance dispersal seems more probable.

The large part of the Blackwater Creek outlier occupies till of the Waimea Formation at about the ice limit of the Waimea Glaciation (Kumara 1 advance) (Suggate, 1965). The centre of the outlier is approximately 2.5 km north-west from the nearest terminal moraine of the $K2_2$ advance (mid Otiran) and 4.6 km from the terminal moraine of the K_3 advance (final Otiran) in the Taramakau valley. Its position, therefore, would not necessarily be influenced by the immediate effects of the glaciers of the Otira Glaciation.

The Blackwater Creek outlier is 13.4 km from the nearest beech forest of the main front in the Arnold valley and there are no known outliers in the intervening area. While seed dispersal and subsequent colonisation over this distance are not impossible (cf. Fig 17) it would be an event of extremely low probability, especially since four long distance dispersal events are needed to establish the four Nothofagus species of the stand. A relict origin is a more likely explanation. The large size of the outlier is consistent with slow expansion from a small stand throughout the Aranuian period, and its position beyond the ice limits of the Otira Glaciation would allow survival during the glacial period. This is the only outlier in north Westland for which there is sufficient evidence to make an Otiran relict origin appear the more probable explanation.

This conclusion appears to conflict with the features of outlier dispersion and species composition which point to a relict origin for a larger group of outliers. For at least some of this group the outlier location in relation to the Otiran ice limits makes a glacial relict origin impossible; others are in locations where survival may have been possible during the Otiran. Three examples would be the

outliers on high outwash terraces in Mawhera State Forest to the north of the Deep Creek outlier (Fig 13). These range in size from 1.0 to 20.1 ha., contain two or three of the fuscoid species and are from 3.8 km to 4.5 km from the main beech forest boundary. These features would be consistent with a relict origin following a major range contraction in the latter part of the Aranuian (but not in the Otiran). There is, however, no evidence of such a contraction in the fossil record (section 5.5) and on these grounds a relict origin for all but the Blackwater Creek is unlikely.

5.4 ORIGINS OF ENCLAVES IN THE NOTHOFAGUS DISTRIBUTION

Within the study area, enclaves of podocarp-hardwood forest occupy higher ground and the central portions of terraces. In the lowlands the enclaves appear to have originated when Nothofagus has spread at a faster rate across flood plains and low terraces compared with hill slopes thereby encircling areas of podocarp-hardwood forest. In the southern Paparoa Range the enclaves have formed subsequent to the spread of Nothofagus around the lower flanks of the range and in the zone between timberline and c 640 m a.s.l.

5.5 AN HISTORICAL RECONSTRUCTION OF NOTHOFAGUS DISTRIBUTIONS IN NORTH WESTLAND DURING THE LATE QUATERNARY

5.5.1 Late Quaternary glaciations, climate and vegetation in North Westland

Vegetation in the South Island was subjected to disruption during the Otira Glaciation by the direct effects of the glaciers and associated erosion and deposition processes, and presumably by the adverse periglacial climate. Willett (1950) proposed a mean depression of the snowline and vegetation zones in the South Island by 3500 ft (1070 m) during the Otiran glacial maxima, which would have the effect of lowering the upper altitudinal limits for trees to close to the present day sea level. However, with the extension of land by the lowering of sea levels by at least 90 m there would be an extensive coastal strip of land available for vegetation refugia during the maximum of the Otira Glaciation (Gage, 1965; Burrows, 1978). Other evidence (e.g. Wardle, 1970; Porter, 1975) suggests that the lowering of snowlines during the Otiran may not have been as great as proposed by Willett (1950). Porter (1975) estimated a depression of 875 m for the Otira maximum and Wardle (1970) a depression in the order of 580 to 790 m. Although mean temperatures were depressed, compared with the present, the periglacial climate was not characterised by severe frost climates and permanently-frozen ground (Gage, 1965). Marine-influenced coastal climates were presumably milder than the inferred inland climates at this time.

There is evidence from the central North Island fossil record for extremes of low rainfall as well as low temperatures during the late Otiran (McGlone, 1980). Fire was common and the climate may have been windier compared with the Aranuian.

The glaciers of north Westland were generally confined to valleys, but in places towards the south of the region the valley glaciers merged to form wide piedmont ice sheets in the lowlands. The extent of the ice cover and the maximum limits of ice advances during the Otira Glaciation and the earlier Waimaunga Glaciation (Suggate, 1965; N.Z. Geological Survey, 1973) are shown in Figure 26. The ice limits for the Waimea Glaciation lie between the limits for the Otira and Waimaunga Glaciations. Most of the glaciers arose in the Southern Alps and flowed westwards along the major valleys into the Grey-Inangahua Depression, forming piedmont ice sheets in the vicinity

Figure 26. Ice limits, Otira coastline and fossil sites in north Westland.

100 m isobath (approx. Otiran maximum shoreline.

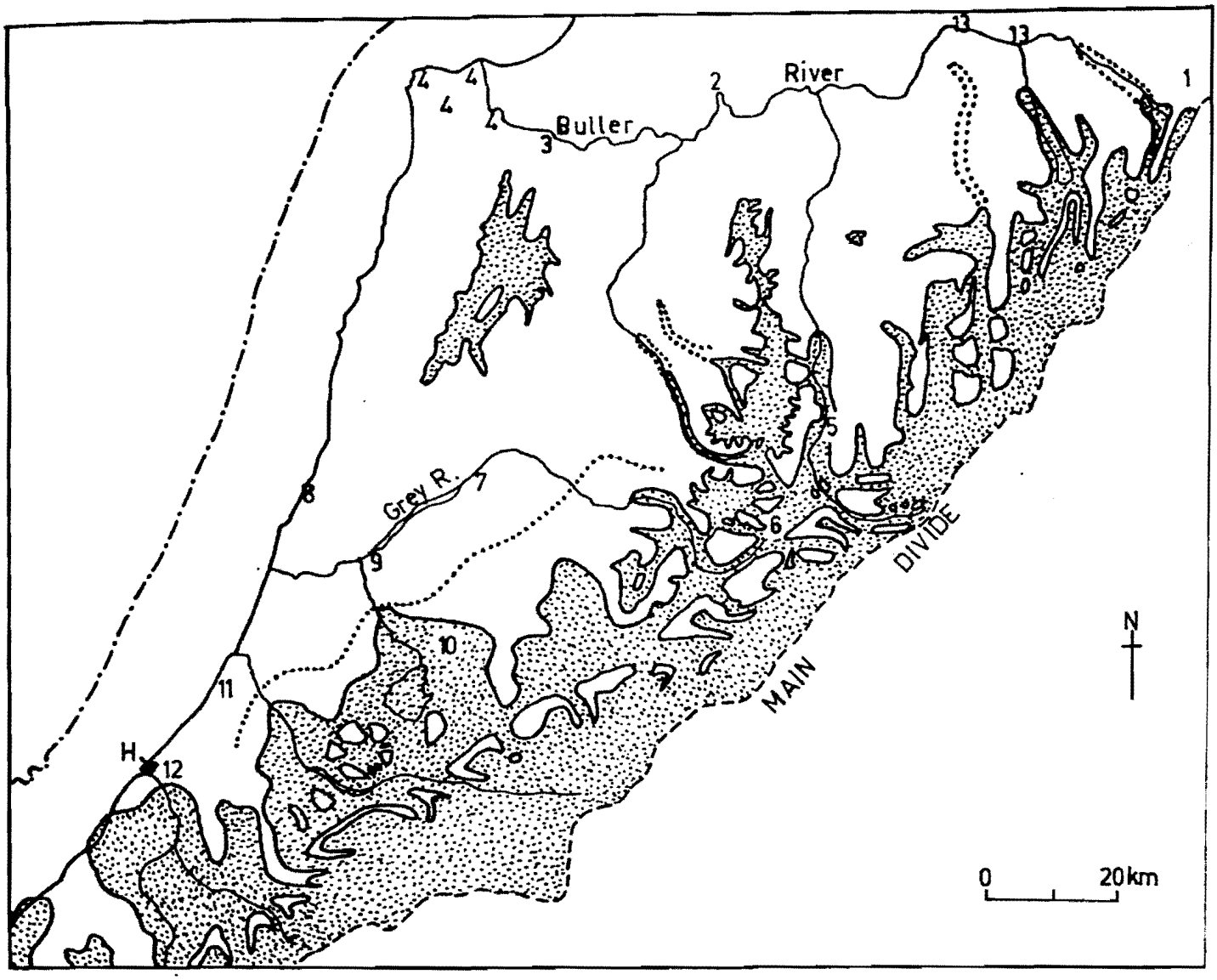
Extent of ice during Otira Glaciation maximum.

Ice limits of Waimaunga Glaciation. (Ice limits after Suggate (1965) and N.Z. Geological Survey (1973).)

H Hokitika.

Numbers refer to fossil sites referred to in text, as follows:

1 Tophouse (Moar, 1971)
2 Pensini Creek (Nathan and Moar, 1973)
3 Ohikanui River (Moar and Suggate, 1979)
4 Westport district (Moar and Suggate, 1979)
5 Ure's Mire, Upper Maruia valley (Moar, 1971)
6 Crooked Mary Ck, Upper Grey valley (Moar, 1971)
7 Totara Flat (Suggate and Moar, 1970)
8 Schultz Creek (Dickson, 1972)
9 Kamaka (Harris, in Suggate, 1965)
10 Bell Hill (Moar, 1971)
11 Sunday Creek (Dickson, 1972)
12 Blue Spur Road (Moar and Suggate, 1973)
13 Upper Buller Gorge (Moar, 1980)


Buller
River
Grey R.
MAIN
DIVIDE
N
0
20km
H
1
2
3
4
5
6
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9
10
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13

of Lake Hochstetter, Lake Brunner and to the south of Hokitika. Minor areas of glaciation were located in the Paparoa and Brunner-Victoria Ranges. Valley glaciers from these areas extended down to the margins of the intervening depression.

Reconstructed profiles of three Westland Valley glaciers (Mathews, 1967; Mabin, 1976) show a rapid loss of elevation from the Main Divide to the Alpine Fault, beyond which the glaciers tend to spread out and lose elevation slowly. These glacier profiles would leave extensive midslopes between the surface of the glacier and the permanent ice cover of the ridge tops. Small side valleys not supporting glaciers would also be ice-free. Within the general areas of glaciation, therefore, extensive areas of mid-altitude sites would remain free of ice (see Fig 26).

Within the north Westland region the largest ice-free area is roughly triangular in shape, bounded by the glaciers associated with the Southern Alps, the extended coastline and the Buller River (Fig 26). A small centre of glaciation in the northern Paparoa Range occurred within the area. Further ice-free areas occurred in the north-west Nelson region to the north. To the south, and further into central Westland, the broad ice sheets occupied most of the land between the Alps and the coast, although some areas such as the coastal hill country near Paringa would have remained ice-free.

The Nothofagus fossil record in north Westland

Fossils of Nothofagus are recorded in sediments from the Oturi Interglacial, the Otira Glaciation and the Aranui Interglacial in north Westland.

Nothofagus was a major forest component during the last Oturi Interglacial in the Westport district (Moar and Suggate, 1979), at Sunday Creek 15 km to the north of Hokitika and at another near-coastal site at Schultz Creek, north of Greymouth (Dickson, 1972). The Sunday Creek record shows that Nothofagus was present at least 8 km further south than its present distribution during the last interglacial.

The Otira Glaciation fossil record in north Westland indicates a predominantly grassland vegetation with some trees and shrubs. There are two exceptions to this general pattern: a minor expansion of

Nothofagus in the Westport district during an interstadial (Moar and Suggate, 1979), and a late Otiran sequence of Nothofagus dominance at Blue Spur Road near Hokitika (Moar and Suggate, 1973). In most Otiran palynological records, Nothofagus pollen is found in low frequencies in association with a predominantly grassland or grassland-shrubland pollen spectrum. These Nothofagus records came from a number of coastal and inland locations (see Fig 26). They are as follows:

Sunday Creek (Dickson, 1972);
Westport district and the Buller Gorge (Moar and Suggate, 1979);
Pensini Creek (Nathan and Moar, 1973);
Totara Flat (Suggate and Moar, 1970);
Kamaka (Harris, in Suggate, 1965);
Upper Buller Gorge (Moar, 1980).

The Buller Gorge record shows a 9% frequency of Nothofagus pollen, including 2% of N. menziesii. Low Nothofagus pollen frequencies are also found in the early Aranuian records from Bell Hill, the Upper Grey valley and the Upper Maruia valley (Moar, 1971). The source of these low Nothofagus pollen frequencies could be small, local stands or larger areas of forest at a greater distance. Near-coastal sites such as the Blue Spur Road area have been suggested as source areas for this pollen (Moar and Suggate, 1973), but the presence of the poorly-dispersed[1] N. menziesii pollen in many of the records supports the presence of local stands.

The spread of forest in north Westland in the Aranuian period has been dated at about 9000 years B.P. at Bell Hill, before 9800 years in the Upper Maruia valley (Moar, 1971) and slightly later than 12 000 years B.P. in the Westport district (Moar and Suggate, 1979). In each locality it was a podocarp-hardwood forest type, with Dacrydium cupressinum dominant, which replaced the grassland or grassland-shrubland vegetation. At Bell Hill, a brief Weinmannia dominant forest phase preceded the Dacrydium cupressinum phase (Moar, 1971).

The spread of Nothofagus dominant forest, as indicated by steep rises in Nothofagus pollen frequencies, has been dated at before7800 years B.P. at Tophouse (Upper Buller valley), at about 6500 years B.P. in the Upper Maruia valley and at about 6000 years B.P. in the nearby

[1] See for example Moar (1970), McKellar (1973).

Upper Grey valley (Moar, 1971).[2] There is a small rise in Nothofagus pollen frequency from about 2400 years B.P. at Nan's Kettle, Bell Hill, indicating the approach of Nothofagus forest from the north. (This site is situated 6.0 km outside the main Nothofagus boundary in north Westland and 1.5 km from the nearest, small outlier). Other Aranuian palynological records from north Westland, at Blue Spur Road (Moar and Suggate, 1973), and the Westport district (Moar and Suggate, 1979) do not show a Nothofagus rise.

In adjoining regions, the prominence of Nothofagus forest has been shown to begin over a wide span of time, ranging from before 10 500 years B.P. at Dew Lakes near Nelson (Dodson, 1978) to 7000-5000 years B.P. for a number of localities in montane Canterbury and c 1000 years B.P. in the Rakaia catchment (Russell, 1980).

The relatively sudden rise in Nothofagus frequencies in pollen diagrams (e.g. Moar, 1971) can be interpreted in several ways. Interpretation is difficult because of the uncertain relationship between pollen frequencies and the extent of the genus in the surrounding vegetation (McGlone, 1980). The rise in Nothofagus frequencies can reflect either arrival at the sample site and/or a general spread in the local and regional vegetation surrounding the site. In each case the genus may have spread from small, local sources or from distant sources. The first alternative would be consistent with slow migration rates and the second with rapid migration. With either alternative, migration from a source area could be influenced by the regional climate or by other factors such as geomorphological instability. The fossil record is inadequate to determine which interpretation is correct. The dated rise in Nothofagus pollen frequencies and other changes in the fossil record at a number of locations in Canterbury within a relatively short period (between 7000 yrs B.P. and 5000 yrs B.P.; Russell, 1980) suggests that the spread of Nothofagus is climatically controlled in that region and is associated with a change to increasing cold or dryness and greater climatic extremes (Lintott and Burrows, 1973; Burrows, 1979). The Nothofagus rise at four sites in the north Westland region is dated from before 8000 yrs B.P. to c 2400 yrs B.P. and is therefore, not synchronous (Moar, 1971). Moar (1971) concluded that there is no evidence from the pollen diagrams for major variations

[2] Corrected radiocarbon dates are shown in Appendix III

in annual precipitation or temperature during the forest phase, although the replacement of podocarp forest by Nothofagus may have been initiated by a change to less equable conditions. The Aranuian fossil record at other sites in north Westland - Bell Hill and Lady Lake - does not show marked vegetation changes during the forest phase indicative of significant climatic fluctuations (Moar , 1971;Pocknall, 1980).

Other New Zealand fossil evidence may reflect a widespread change to droughtier and colder conditions after about 5000 yrs B.P. with some intensification of more extreme conditions after about 3500 years (McGlone and Moar, 1977; McGlone and Topping, 1977) but the evidence for this change in South Island localities is not as clear as for North Island localities (McGlone, 1980).

Given the limitations of the presently available Aranuian fossil record in north Westland, it is difficult to draw conclusions about the postglacial spread of Nothofagus. There is no clear evidence for climatic control of Nothofagus spread and either slow expansion from local refugia or rapid migration from distant refugia would be consistent with the fossil record.

5.5.2 Evidence from present-day distributions and migration patterns

The orientation of the migration routes derived from present species distributions (section 4.7) points to a number of source areas for the past expansion of beech forest. Coastal origins near Runanga and to the north of Barrytown appear likely for expansion into the southern end of the Paparoa Range and across the range into the margins of the Grey-Inangahua Depression (see Fig 24). Within the Depression a number of source areas in the central area and along the eastern margins, with possible migration from the upper Ahaura Valley, are suggested. An east to west migration across low passes in the Southern Alps from Canterbury beech forests is also likely at several places from Worseley Pass in the south to Ada Pass in the north of the region.

The Nothofagus species distributions in the study area provide support for the existence of at least two source areas for all four species, separate from the inferred major source areas to the north and east. The first is the Blackwater Creek outlier which is widely disjunct

from the main area of distribution and which appears to be of relict origin (section 5.3). The second is the Runanga district which is partially separated from beech forest to the north and east by large enclaves of podocarp-hardwood forest. All four Nothofagus species are present in both areas.

The absence of N. menziesii in Granville State Forest and nearby areas close to, but within, the main beech forest boundary (Fig 14) shows that these were not source areas for this species. In view of the greater ecological amplitude of N. menziesii in colder climatic regimes compared with the other species, it seems less likely that these areas were source areas for the fuscoid group of species as well.

5.5.3 A reconstruction of Nothofagus distribution in the study area during the Aranuian period

In this section a model of the postglacial distribution of Nothofagus in and adjoining the study area is described. The model covers the position of glacial period refugia and the direction and extent of postglacial spread from the refugia. Several lines of evidence are used, including the fossil record (section 5.5.1), the present Nothofagus species distributions (section 4.2) and the known dispersal characteristics of Nothofagus (section 5.2). The assumptions forming the basis of the model are described and justified below.

Limitations to migration during the Aranuian period

Under present conditions the Nothofagus range is expanding on most sites in the study area. Judging from the orientation of the Nothofagus boundaries and the dispersion of outliers, this expansion has continued in the recent past, possibly for at least 1000 years. The fossil record indicates expansion at different times throughout the Aranuian forest phase in north Westland. There is no definite evidence from the three relevant fossil sites to show that the spread of Nothofagus was limited by unfavourable climatic conditions during this period.

In view of the fossil and distribution evidence, and the ability of the Nothofagus species to occupy a wide range of growing sites under

most climatic regimes in the western South Island, it would appear that the spread of Nothofagus in north Westland was not controlled by the relatively minor climatic changes in that region over the past 10 000-9 000 years. Consequently, for the purposes of this model it is assumed that Nothofagus has spread continuously at a constant rate throughout the study area during the Aranuian forest phase. The possible effects of climatic changes such as the postulated increase in droughtiness and decline in temperature at c 6000-5000 yrs B.P. are not, therefore, included in the model. If climatic changes during the forest phase were effective in preventing the spread of Nothofagus then the time available for the postglacial expansion would be less than 10 000 years and the total expansion of range would be correspondingly shorter than assumed. A 10 000 year period is assumed to be available for expansion on the basis of the three available dates for the spread of forest in north Westland (section 5.5.1).

Faster rates of migration than those evident in the present day forests would imply a different set of vegetation, soil and climatic conditions in the past. More rapid migration could result from greater air turbulence (leading to a wider dispersal of seed) and from invasion of more open-canopied vegetation or vegetation subject to a greater degree of disturbance (creating more opportunities for seedling establishment). There is, however, no evidence for a more turbulent or geologically more unstable environment, or more open-canopied vegetation in the study area in the past 10 000-9 000 years from the fossil record (section 5.5.1) or from geological evidence. One geomorphological study in the study area confirms the stability of conditions during this period. The slope characteristics of hill country at Notown in the lower Grey valley provides evidence for the existence of a complete and continuous vegetation cover throughout the Aranuian period (O'Loughlin and Gage, 1975). The limited colonisation of areas disturbed by human activity in recent decades (section 5.2.3) suggests that widespread vegetation disturbance does not necessarily lead to major extensions of range. This situation may have pertained in the more distant past.

The above considerations lead to the assumption in the model that migration rates in the study area in the past 10 000 years were unlikely

to have been greatly different from rates in the recent past. The rate of migration is limited throughout postglacial time by the inherent migratory capability of the Nothofagus species and by the nature of the environment during this period.

Construction of the model

The model is based on a combination of evidence from present Nothofagus species distributions, inferred migration routes and estimated postglacial migration distances. Areas covered by Otiran glaciers were not considered as possible refugia locations.

Total postglacial migration distances were derived from the product of the mean rate of marginal spread (section 4.7), the relative rates of migration on different sites (section 4.7) and the time assumed to be available for migration during the postglacial (10 000 years).

This gives total migration distances in the order of 1 km (0.7 km to 1.3 km using the 95% confidence limits of the mean rate of marginal spread, Table 12) for expansion across hill slopes and up to 4.7 km upstream along flood plains (based on six valleys containing protrusions of beech forest, section 4.7). Longer migration distances are possible downstream along flood plains (for example 9.8 km using the boundary orientation in the Taramakau Valley). Migration distances along intermediate and high terraces would be of similar magnitude to those upstream along flood plains. The contribution of outlier formation to migration was considered to be significant only in the upland zone where an additional migration distance of 5 km is possible (based on the length of boundary protrusions in the upland zone, sections 4.2 and 4.7). Additional extensions of range in the lowlands by outlier formation and expansion would, however, be possible in local areas, especially along flood plains with active aggradation and degradation.

A total migration distance of 15 km or up to 30 km downstream along the flood plains of the Grey River and Deep Creek is possible given the likely points of entry onto the flood plains and likely migration routes (sections 4.9 and 5.3).

The model

Nine glacial period refugia for Nothofagus are postulated within the study area. The locations of the proposed refugia and inferred major migration routes from them are shown in Fig 27.

The refugia fall into two groups. The first group comprises five refugia which are proposed on the basis of the orientation of the existing beech forest boundary in relation to topography, species composition, possible migration routes and estimated migration rates. These refugia are at Blackwater Creek, Runanga, middle Grey-Inangahua Depression, Waipuna and Granite Ridge. All four Nothofagus species are present.

The second group contains four refugia (Upper Nelson Creek, Lower Nelson Creek, Lake Hochstetter and Arnold River) proposed on the basis of the estimated migration rate across high and intermediate terraces which gives a likely postglacial total migration distance of less than 5 km. The evidence for this group of refugia is less substantial than that for the first group which are supported by evidence from the boundary orientation in the vicinity (see section 5.5.2). The first group of proposed refugia contains the four Nothofagus species, whereas in the second group N. menziesii is missing. The presence of N. menziesii, which has a more restricted distribution than the other species in the lowland forests of the study area increases the likelihood of an area being a refugium.

The postulated refugia areas are described in turn:

(a) Blackwater Creek

This refugium is located on partially-dissected, high outwash terraces and till of the Waimea Formation (see section 5.3). At the time of initiation of postglacial beech forest expansion the refugium was presumably restricted to a small area near the centre of the present outlier. The altitudinal range is from 60 to 170 m a.s.l.

(b) Runanga District

This area is largely coastal and comprises small areas of marine and outwash terraces and dissected hill country of greywacke, sandstone and coal measures (Bowen, 1964). The altitudinal range of this proposed refugium is from sea level to 400 m a.s.l.

Figure 27. Postulated Nothofagus glacial refugia and postglacial migration routes in the study area.

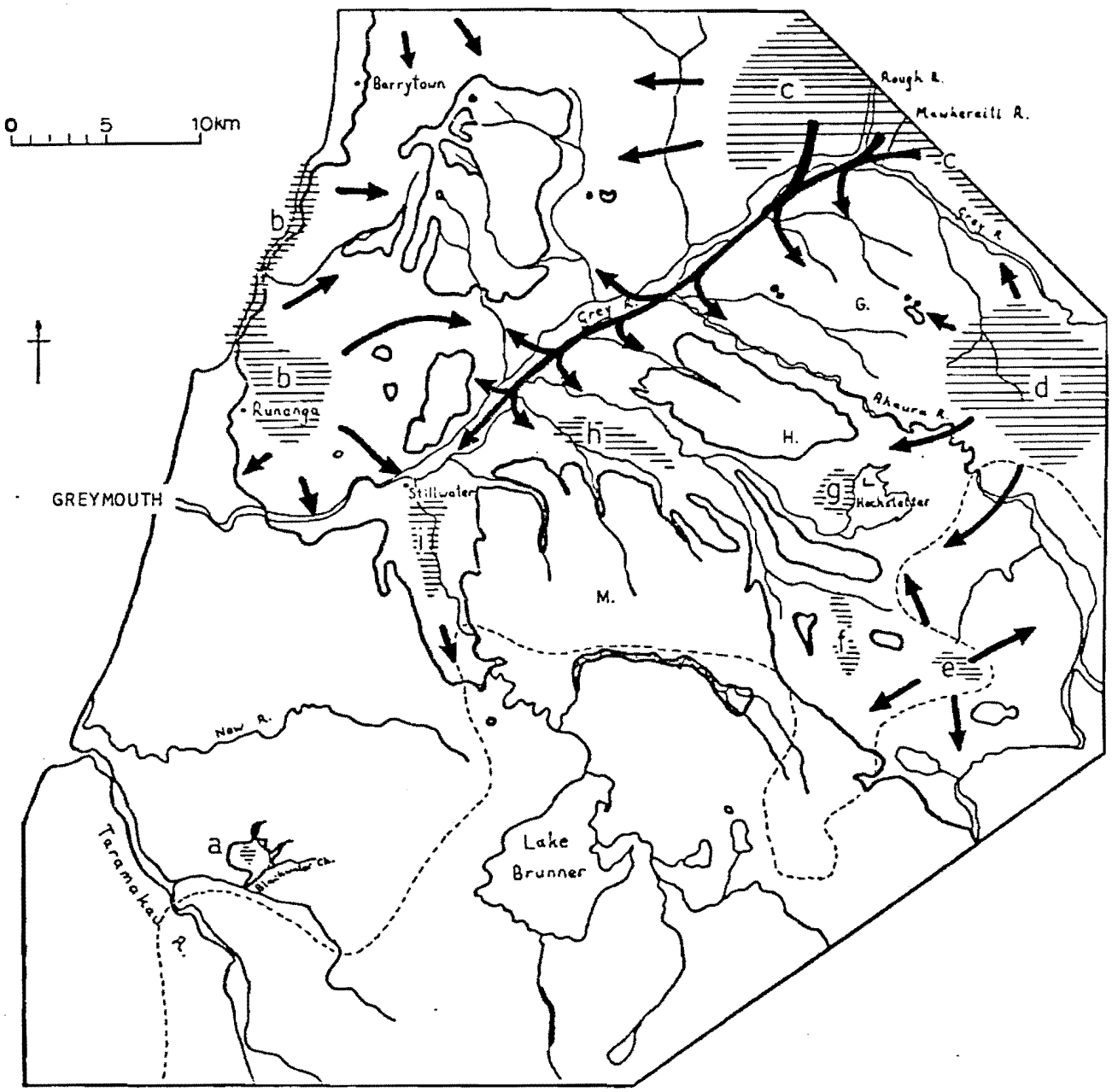
Postulated refugia locations

a - Blackwater Creek
b - Runanga district
c - Middle Grey-Inangahua Depression
d - Waipuna terraces
e - Granite Ridge
f - Upper Nelson Creek terraces
g - Lake Hochstetter terraces
h - Lower Nelson Creek terraces
i - Arnold River terraces

Postulated migration routes

----- Otiran maximum ($K2_2$) ice limits

G. - Granville State Forest
H. - Hochstetter State Forest
M. - Mawhera State Forest


0 5 10km
Barrytown
Rough R.
Mawheraiti R.
C
b
Grey R.
G.
Runanga
H.
Rahoura R.
d
h
GREYMOUTH
Stillwater
g
Lake Hochstetter
M.
f
e
Now R.
Taramakau R.
a
Lake Brunner

(c) Middle Grey-Inangahua Depression

The area of dissected hill country and broad outwash terraces forming the middle portion of the Grey-Inangahua Depression between Ikamatua and Reefton appears to be the source area for a major migration route southwards along the flood plain of the lower Grey River. Refugia could have been located throughout a wide area drained by the Rough, Mawheraiti and Snowy Rivers and their tributaries together with the middle section of the Grey River.

Proceeding southwards along the Grey River flood plain in the study area, the adjoining hill country is progressively less completely occupied by beech forest. This pattern is illustrated in a sequence from Granville State Forest to Mawhera State Forest (Figs 9 and 10). Granville State Forest contains only a scattering of small podocarp-hardwood forest enclaves, whereas in Hochstetter and Mawhera State Forests beech forest is largely marginal to the hill country where it extends only as valley 'fingers' or occasional outliers. The Granville State Forest hill country is more accessible to invasion by beech forest because all hill slopes are less than 1 km from the numerous small flood plains of the tributary streams in the area. By contrast, Hochstetter and Mawhera State Forests are of different relief; hill slopes are longer, the streams mostly engorged in their middle and upper reaches and fewer tributary flood plains are available as invasion routes. The north to south migration pattern, therefore, is modified by the topography and drainage patterns of the country being invaded.

The total migration distance from the margins of the proposed refugium along the broad flood plain of the Grey River is at least 15 km and possibly as much as 30 km, but the sideways migration distance away from the flood-plain ranges from 0.5 km to 10 km. The lowest altitudes in the proposed refugium are from 150-200 m a.s.l.

(d) Waipuna Terraces

These rolling, slightly-dissected outwash terraces of the Waimea Formation lie between the dissected hill country to the west and

and the Mount Elliot mountain block to the east. Drainage is by the Waipuna Creek to the north and to the Ahaura River to the south.

Total migration distances from the margins of the refugium would extend as far as 7 km on to the terraces to the east of Lake Hochstetter and for shorter distances in other directions. The altitudinal range of this area is from 210 to 400 m a.s.l.

(e) Granite Ridge

This refugium is suggested by the orientation of the boundary in the Lake Ahaura region and, in particular, by the occupation by beech forest of all but the western slopes of this 8 km-long ridge.

The ridge, which is formed from granite parent material, would be close to the ice margins of the Otiran glacial advances (Suggate, 1965). Expansion from this area would extend for up to 5–6 km across the adjoining terraces in all directions. The altitudinal range of Granite Ridge is 340 to 590 m a.s.l.

(f) Upper Nelson Creek terraces

A refugium is suggested on this large area of gently-rolling outwash terraces of the Waimea and Loopline Formations. This area lay outside the ice margins during the Otiran glacial maximum (Suggate, 1965). The altitude of the area is about 300 m a.s.l.

(g) Lake Hochstetter terraces

These gently-sloping terraces with deeply-incised streams extend from the western shores of Lake Hochstetter to the base of the hill country of Hochstetter State Forest. The terraces have been assigned to the Waimea Formation in common with the Waipuna terraces (Bowen, 1964). The altitude of the area is about 300 m a.s.l.

(h) Lower Nelson Creek terraces

These intermediate terraces of the Loopline Formation lie to the east of Ngahere. The area is about 90 m a.s.l.

(i) Arnold River Terraces

Lying on both sides of the lower Arnold River, these gently-sloping terraces are assigned to the Loopline Formation. The area is about 60 m a.s.l.

If, as an alternative model, it is assumed that only the first group were glacial period refugia, then total migration distances would be greater than those indicated if the second group of proposed refugia were also present. Thus migration distances from the first group of refugia across terraces would be in the order of 10–15 km, involving, for example, migration from Granville around the head of Lake Hochstetter and across the terraces to the west of the lake. This range is well in excess of the 5 km range indicated from inferred relative migration rates (section 4.7). On other sites, too, migration distances would be significantly greater than those estimated on the basis of inferred migration rates. Thus migration distances of 5 km rather than 1 km across hill slopes and 30 km rather than 15 km downstream along watercourses would be indicated for this alternative model.

Although the proposed coastal refugium at Runanga could have extended out on to the coastal plain uncovered by the lowered Otiran sea level, refugia along the extended Otiran coastline need not be postulated to explain the present Nothofagus distribution patterns. A postglacial contraction of range away from the coastline is possible since many coastal sites are not occupied by Nothofagus today (Fig 9).

The fossil pollen record at Blue Spur Road, Hokitika indicates the presence of a Nothofagus dominant forest refugium in that locality which survived during the late Otiran but became extinct at the time of Dacrydium cuppressinum spread in the early Aranuian (Moar and Suggate, 1973; Moar, 1980). This locality is some 25 km to the south west of the proposed Blackwater Creek refugium.

5.5.4 The Otiran and Aranuian distribution of Nothofagus in the South Island

Otiran refugia

Application of the model of the distribution of Nothofagus refugia (previous section) to the remainder of the South Island would imply a wide distribution of refugia within or close to the areas now occupied

by Nothofagus. There is evidence from the fossil record for Nothofagus refugia in a number of South Island localities. Refugia in the Canterbury foothills of the Southern Alps have been suggested by Molloy and Cox (1972), Lintott and Burrows (1973), Moar and Lintott (1977) and Russell (1980) on the basis of the early appearance of Nothofagus in the Aranuian fossil record. Similar evidence is found in postglacial deposits in the upper Clutha valley (McKellar, 1960), at Dew Lakes near Nelson where a mixed Nothofagus-podocarp forest was present since 10 500 yrs B.P. (Dodson, 1978) and at Tophouse, Lake Rotoiti, where a Nothofagus-dominant forest was present from before 8000 yrs B.P. (Moar, 1971). Wardle and McKellar (1978) consider that N. menziesii leaves and other macrofossils from the head of Milford Sound, Fiordland, dated at 7490 yrs B.P. provide evidence for Otiran forest refugia in the south of the South Island. The fossil record is, however, inadequate to confirm the actual locations of Otiran refugia.

Further refugia localities in the Paringa and Jacksons Bay districts in south Westland have been suggested on the basis of present day Nothofagus species distributions (June, 1977; Wardle, 1980 a).

The close dispersion of refugia described in the distribution model for the study area would not appear to be possible in the adverse environment of the glaciated areas of the South Island. With maximum postglacial migration distances of 15 km the refugia would have to be located in mid-slope positions in the glaciated montane valleys at altitudes greater than 450 m a.s.l. For north Westland this would involve unlikely refugia locations in the upper Taramakau, the upper Maruia and the upper Grey valleys, for example.

If refugia were located just outside the main area of Otiran glaciation in the north Westland region (see Fig 26) the postglacial migration distances to the present limits of distribution at the head of montane valleys in the Southern Alps would be up to 45 km. In this situation postglacial migration rates would have been several times faster than those derived from the study area. Refugia could be located beyond the limits of the Otiran glaciers in the Grey-Inangahua Depression and in the lower sections of the montane valleys. One possible refugium is indicated by the pre 8000 yr B.P. record of Nothofagus dominance in a pollen sequence at Tophouse (Moar, 1971) located 5 km from the limits of the Otiran glacier which occupied

the Travers valley (Suggate, 1965).

There is other evidence from the South Island for postglacial migration distances greater than 4 5 km. The upper Taramakau Nothofagus forests appear to have originated from the eastern side of the Southern Alps (section 4.9). If it is assumed that this postglacial spread originated in refugia beyond the maximum limits of the Otiran glaciers (see Gage, 1977) in the Canterbury foothills near the Oxford Hills, then the total postglacial migration distance in this case would be 85–90 km (via the Poulter Valley and Worseley Pass).

The various radiocarbon dates and interpolated estimates for the spread of Nothofagus in the Cass region (Moar, 1971; Lintott and Burrows, 1973; Moar and Lintott, 1977; C J Burrows, pers. comm. 1981) suggest a more rapid postglacial spread. Nothofagus is considered to have spread at Kettlehole Bog at Cass, possibly from local refugia, in the period c 6000 years B.P., at the upper Bealy River between 5180 ± 90 and 7000 years B.P. and at the upper Waimakiriri around 4830 ± 90 years B.P. Local glacial period refugia are unlikely at the latter two locations where Nothofagus is now extensively distributed. These locations are about 25 km up the Waimakiriri Valley from the Kettlehole Bog site. If migration proceeded from the vicinity of Cass to the upper valley sites, the 25 km could have been traversed in as little as 1000 years.

In the Paringa district likely post/glacial migration from refugia near the coast and up the Landsborough Valley has been traced by Wardle (1980 a). The total postglacial migration distance in this case is 65–70 km.

The more rapid migration evident in these examples could be a result of vegetation and site differences during the postglacial between the lowlands of the study area and the montane valleys of the Southern Alps. Migration is likely to be more rapid when the vegetation being invaded is low and/or open-canopied or subject to gross disturbance, and when bare surfaces are continually being exposed on slips or along river banks. Seed could be dispersed over longer distances than usual by being blown along the shingle river beds. These conditions are a feature of at least parts of the montane valleys of the Southern Alps.

Origin of the central Westland Nothofagus gap

Nothofagus is absent from large areas of its potential range in the South Island. The major discontinuity of range is in the middle of the island where Nothofagus is completely absent from a 165 km section of central Westland and partially absent from a further 20 km section to the north and 80 km to the south. This is paralleled by an absence from a 120 km strip just east of the Main Divide from the north side of the Tasman River to the Wilberforce River (Fig 2; N.Z. Forest Service, 1974).

This large 'gap' in the Westland distribution of Nothofagus has been attributed to the effects of the Pleistocene glaciations (Cockayne, 1926; Willett, 1950). The area from which Nothofagus is absent largely corresponds with the highest section of the Southern Alps from which the most extensive glaciers arose. This area was subjected to more intense glaciation than peripheral areas to the north and south. The width of land between the Main Divide and the coastline also varies along the length of Westland and is at a minimum in the central section. These factors point to the greater likelihood of refugium survival around the northern and southern ends of the Southern Alps than in the central section.

The hypothesis linking the Westland Nothofagus 'gap' with the disruptive effects of the Otira Glaciation cannot be sustained in detail, however. Areas to the north and the south of the 'gap' were also extensively glaciated and yet today are occupied by Nothofagus. There were a number of ice-free areas within central Westland where survival during the stadials of Otira Glaciation might have been possible, particularly in areas associated with the extended coastline of that period. These include the extensive hill country near Ross, much of the southern end of the Grey-Inangahua Depression, and the coastal morainic country between Abut Head and Gillespie Point. These areas were located outside the Otiran ice limits (see N.Z. Geological Survey, 1973).

The absence of Nothofagus refugia from apparently suitable locations in central Westland may be explained if a longer time span than the Otira Glaciation is considered. The absence of refugia in these locations, as inferred from the present absence of Nothofagus, means that it is unlikely that Nothofagus had occupied all of its

potential range in central Westland by the end of the Oturi Interglacial, and possibly the previous interglacial periods. The locations of refugia at the time of the Otiran would reflect the cumulative effect of a succession of range contractions during each glaciation and of range expansions during each interglacial. Some range contractions may have been greater than others because of the relative length and intensity of the associated glaciation. The extent of range expansions would also vary, according to the length of the periods available for expansion and the conditions prevailing during those periods.

The present geographical limits of Nothofagus in north and south Westland can therefore be seen as the end result of slow expansion from Otiran glacial period refugia whose positions were determined by the relative intensity and duration of a sequence of adverse glacial and favourable interglacial periods.

5.6 SEEDLING ESTABLISHMENT, GROWTH AND SURVIVAL

The size of a seedling population is determined by the rate of input through seedling establishment and the rate of output through mortality and growth into the next largest size class. Small seedling population densities of the five species studied in permanent quadrats (section 4.11) are proportional to establishment and outgrowth rates, but are not proportional to observed mortality rates. The species with low seedling densities, rata, also has the lowest mortality rate and the beech species with relatively high densities have high mortality rates. Miro has low densities and high mortality. Intra-specific competition may operate to a limited extent at this level.

Early establishment

The rates of early establishment observed in permanent plots are a function of germination and survival throughout the seedlings' first growing season. The large fluctuations in establishment rate observed from 1975 to 1977 in some species (section 4.11.2) appear to be, at least in part, the result of annual fluctuations in seed production. The high rate of establishment in 1977 of hard beech and red beech followed a previous season of prolific flowering and seed production for these species in the study area and throughout north Westland (Franklin, 1977). Records of annual seed production are not available for rimu, but this species is known to have large annual fluctuations in seed output with infrequent heavy seed crops in Westland and elsewhere (Travers, 1961; Beveridge, 1964; 1973; Franklin, 1968). Periodicity in seed production is less marked in miro (Beveridge,

1973). In Nothofagus there is negligible seed fall in some years and in other years massive seedfalls at intervals ranging from two to ten years (Poole, 1948; Wardle, 1970b). In north Westland heavy seedfalls in red beech have been noted at intervals of two to five years, and in hard beech from three to seven years (Kirkland, 1961; Johnston, 1972; Franklin, 1977a).

The results of the present study seem to conflict with those from a study of sugar maple (Acer saccharum) where large fluctuations in seed production from year to year did not result in corresponding differences in the numbers of seedlings in each year's age group when assessed in later years (Hett, 1971). This indicates the importance of density-dependent mortality in sugar maple seedlings compared with the species under study here.

Microsite requirements

Differences in the range of microsite types in which the seedlings of each species can become established are considerable (section 4.11.3). In general, there is no dependence on a particular type of microsite, but rimu, rata and red beech seedlings have a definite preference for fallen logs and rimu and red beech establishment is less frequent beneath a low shrub layer. First year seedlings of rimu and rata in particular have difficulty establishing in leaf litter. These species have slow initial growth rates from small seeds and are vulnerable to dessication during the early stages of growth. In contrast, the rapid initial growth of miro seedlings means that germination and early establishment of this species is successful on a wider range of microsites including deep litter. Miro has the least specific microsite requirements for early establishment.

Microsites lacking litter, i.e. where the humus or mineral soil layers are exposed or the ground surface is covered by bryophytes or rotting wood, and microsites where an overhanging low shrub layer is absent are the most favourable for the early establishment of all species. This type of microsite is generally not common but is found in places throughout the stands. Observations on seedling abundance and distribution suggest that not all suitable microsites are occupied by seedlings of the canopy tree species. The availability of suitable microsites does not appear, therefore, to limit the numbers of seedlings which become established. Rata may be the exception because of the narrow microsite requirements of this species, but many fallen logs which are apparently suitable for seedling establishment have not been colonised by this species.

The inhibitory effect of a continuous leaf litter has been observed in a wide range of northern temperate and tropical tree species (Keever, 1973; Ng, 1978) and also in New Zealand tree species. Early establishment of Nothofagus seedlings is most successful where the humus layer has been removed by soil disturbance (Conway, 1952; Kirkland, 1961). Similar observations have been made for rimu establishment (Burns, 1931; Franklin, 1969). Continued survival of rimu seedlings is poor where there is a dense regrowth of trees, shrubs and ferns following distrubance (Brown and Stichbury, 1973). These observations apply to subcultural treatments of both terrace and hill slope rimu stands. Cameron (1963) observed the failure of rimu seedlings to survive in thick humus layers occupied by the roots of mature podocarp trees in dense podocarp stands at Whirinaki forest, North Island. Rimu seedlings growing in this

situation, and particularly those in conditions of low light, had poorly developed root systems which did not penetrate the humus layer.

Favourable microsites for continued seedling development, as shown by the preferred microsites for large seedlings of rimu, rata and hard beech have in common an absence of established dense fern and shrub layers. The occurrence of large rimu seedlings around the margins of depressions which are often water-filled may be a consequence of the ability of the seedlings to withstand waterlogged soil conditions and the inability of other competing species to become established or to grow on the same microsite.

Mortality

The major causes of seedling mortality were difficult to identify but it is likely that most deaths of newly germinated seedlings are caused by fungal pathogens, ('damping off' and root rot) especially in moist, shaded microsites (Vaartaja, 1952; Tappeiner and Helms, 1971), and by dessication during dry periods especially in microsites exposed to full sunlight. In a survey of tropical tree species, the species with small seedlings were found to be more susceptible to 'damping off' and dessication than species with large initial seedling sizes (Ng, 1978).

For large seedlings most deaths appear to result from prolonged periods of growth suppression. Mortality is an infrequent occurrence affecting individual seedlings; none of the species studied were observed to be subject to widespread episodes of mortality. Browsing by introduced animals is not a significant cause of mortality, except in the localised areas where goats are present.

Mortality rates of small seedlings of each species vary significantly from year to year, but the larger seedlings do not show this pattern. The annual trend for small seedlings is consistent with mortality caused by climatic factors and related to annual fluctuations in these factors. It also indicates that small seedling mortality is influenced by different factors from those affecting large seedlings.

The effect of microsite type on mortality varies from species to species. For small rimu and hard beech seedlings mortality is lower in less shaded microsites on the ground and on fallen logs. For large seedlings, the response is more variable. Large miro seedlings are subject to greater mortality under a canopy cover (section 4.11.4).

Rotting fallen logs and stumps are elevated microsites which are seldom fully occupied by competing ferns and shrubs or penetrated by the root systems of canopy trees. The higher mortality in more shaded microsites points to an influence of light intensity on seedling survival. The favourability of the rotting wood microsite also indicates the importance of root competition from ground, subcanopy and tree species. Other factors which may affect the favourability of the rotting wood microsite are the water retention capacity of rotten wood, the frequent bryophyte cover and the availability of mineral nutrients from wood decay (June, 1974). The preference of seedlings for fallen logs and stumps has been observed elsewhere for red beech, silver beech and rimu seedlings (Wardle, 1963b; June and Ogden 1975; Wardle, 1980a).

Height growth

The ability of seedlings to grow rapidly in height to avoid being overshadowed by competitors, and the ability to withstand suppression under the canopy of other plants are important attributes in successful recruitment to the canopy. Red and hard beech seedlings have the fastest height growth rates of the five species studied in undisturbed forest (section 4.11.5). These species can grow as fast as Quintinia and Kamahi which also grow rapidly in canopy openings. Rimu and miro are unable to grow as rapidly. Rata also has slow average growth rates but large seedlings are capable of rapid growth and this species is occasionally observed to colonize large canopy openings together with the beech species, Quintinia and kamahi.

The seedling populations have significant proportions of suppressed individuals showing little growth in height from year to year and dieback of the main stem. These seedlings are mostly found below canopy and/or subcanopy foliage layers, but seedlings suddenly exposed to full sunlight in large canopy gaps can also suffer from dieback. Suppressed seedlings of all species are capable of surviving for a number of years with low or negative growth rates and still respond with more rapid growth when growth conditions change. Large seedlings of red beech and rata show a significant response to canopy opening with faster growth in canopy gaps. Kamahi and Quintinia seedlings are also capable of surviving periods of suppressed growth and of responding to canopy opening by greatly increased height growth.

The presence of seedling populations with a high proportion of suppressed seedlings able to respond by increased height growth when canopy gaps are formed has been

described for a wide range of tree species. This characteristic has been previously noted in hard beech and red beech (Kirkland, 1961) and rimu (Beveridge and Franklin, 1979). It is found in many shade tolerant species in northern temperate forests, for example Fagus grandifolia and Acer saccharum (Keever, 1973; Marks, 1974; Borman and Likens, 1979), and in tropical forests (Poore, 1968; Whitmore, 1975).

The seedling demographic characteristics of each of the five species studied in detail are summarized in Table 36. Hard beech and red beech have high seedling densities, wide microsite preferences and fast to medium growth rates. Quintinia and kamahi also share these characteristics. Rimu, miro and rata have low seedling densities which are associated with low to very low rates of early establishment. These species differ in other respects, however. Small miro seedlings have very wide microsite preferences whereas rimu and rata have more restricted microsite requirements. The early height growth of miro is much more rapid than that of rimu and rata.

TABLE 36 Summary of demographic characteristics of seedlings of species studied in permanent quadrats and tagged populations.
(for each characteristic, where appropriate, significant differences are noted by different descriptive terms)

	Rimu	Miro	Rata	Hard beech	Red beech
Population size	small	small	small	large	medium
Establishment rate	low	v.low	v.low	high	medium
Microsite preferences	narrow	v. wide	v. narrow	wide	wide
Initial growth rate	slow	v. fast	v. slow	medium	medium
Large seedling growth rate (cm/yr)	slow (0.81)	slow (0.86)	medium (1.47)	medium (1.43)	fast (3.65)
Max. annual growth, large seedlings (cm)	low (5.25)	high (10.5)	high (12.5)	high (14.1)	high (22.5)
Growth response in canopy gaps, large seedlings	-	-	+	-	+
Mortality rate, small seedlings (%)	medium (16.4)	medium (16)	low (4.0)	medium (13.3)	high (23.3)
Mortality rate, large seedlings (%)	medium (4.1)	medium (2.4)	Low-medium (1.3)	high (5.0)	medium (2.0)
Population turnover (%) (small seedlings)	43	62	17	54	70

During the first few years of growth seedlings of all five species have a high shade tolerance[1] with miro having a greater tolerance than the other species. As seedlings age, fewer survive beneath the canopy of dense shrub and ground layers, and species differences in tolerance become apparent (section 4.11.3).

A comparison of the germination and early growth requirements of the five canopy tree species studied (Table 36) reveals a relationship between initial growth rates, seed sizes and the specificity of microsite requirements. Species with narrower microsite requirements, particularly rata and rimu, have smaller seeds and slow initial height growth rates. These species also tend to have lower seedling densities and a greater patchiness of distribution.

Ng's (1978) survey of tropical tree species also shows a correlation between small seed size, small initial seedling size and difficulty in early establishment, particularly in litter. Seedlings developing from small seeds have an advantage in being able to find a foothold in small crevices. Grime and Jeffrey (1965) also found a correlation between seed size and seedling height growth rates for a number of northern temperate tree species. Smaller seedlings also had higher mortality rates.

[1]The concept of shade tolerance refers to the ability of a species to survive and grow under its own canopy and that of other species.

5.7 REGENERATION PATTERNS AND REPRODUCTIVE STRATEGIES

Three major kinds of regeneration pattern can be recognised in forest tree species:

(1) continuous regeneration involving the replacement of single canopy trees as they die by shade tolerant individuals in the subcanopy;

(2) gap-phase replacement (Bray, 1956) in which individual canopy trees or groups of trees are replaced by seedlings and saplings which colonise or develop within the canopy opening thereby created;

(3) large-scale replacement following the destruction of a large area of the forest canopy by infrequent catastrophic events such as fire, gales, snowfall, drought, predator attack, etc.

In a spatial sense the distinction between gap-phase and large-scale replacement is one of degree; disturbances can adversely effect the forest canopy on a scale ranging from the canopy space of a single tree to extensive areas covering many hectares. In both gap-phase and large-scale replacement tree senescence can be an important factor, but exogenous factors such as gales, snowstorm and fires are more important in large-scale replacement.

The classification of regeneration patterns, while providing a useful basis for species comparisons, does not adequately emphasize the individual regeneration characteristics of each species. In forest regeneration a sequence of life cycle stages is involved in the invasion of canopy gaps left by dead canopy trees. These stages include seed production, seed dispersal, germination and growth through the subcanopy. Each species is likely to differ in its requirements for growth and survival at each stage, in its morphogenetic characteristics (e.g. rate of seed output, adaptations for seed dispersal and height growth rate), and in its response to competition from other plants, animal browsing, pathogen attack and climatic stresses. For each species these characteristics can be said to define a unique 'regeneration niche' as a component of the overall niche of a plant species (Grubb, 1977).

The predominant and secondary regeneration patterns of the major canopy tree species in the study stands are summarized in Table 37.

TABLE 37 Predominant and secondary regeneration patterns of the major canopy tree species in the study stands

Species	Regeneration Pattern		
	Continuous	Gap-phase	Large-scale[1]
Rimu	++		
Rata	+	++	+
Miro	++		
Hard beech	+	++	+
Red beech		++	+
Kamahi	+	++	+
Quintinia		++	+

++ predominant pattern

\+ secondary pattern

[1] refers to natural disturbance only

Rimu and miro have predominantly continuous regeneration and the other species predominantly gap-phase regeneration. Of this second group, rata, hard beech and kamahi have continuous regeneration as a secondary pattern. Rimu and miro exhibit high degrees of shade tolerance in the subcanopy, rata, hard beech and kamahi have intermediate characteristics (rata being the most shade tolerant of this group) and red beech and Quintinia are light demanding. The species with predominantly gap-phase replacement are also able to regenerate prolifically following large-scale stand disturbance by windthrow.

The creation of gaps in the forest canopy leads to different regeneration responses depending on the size of the gap created. Small gaps created by the death or senescence of canopy trees and less than about 50 m^2 in area can be filled by branch outgrowth from canopy trees adjacent to the gap. Small canopy gaps allow a greater amount of direct sunlight to the forest floor than a closed canopy where only sunflecks reach the floor (Evans, 1956; Whitmore, 1975). Large canopy gaps could also affect the light regime for some distance around the gap by increasing the amount of reflected and possibly direct sunlight reaching the forest floor. The diameter growth rates of rimu in the subcanopy

show a response to nearby openings in the canopy (section 4.12.1). Small, temporary gaps in the canopy although soon filled by canopy outgrowth would appear to be important for continued growth through the subcanopy of the shade-tolerant species with the continuous mode of regeneration.

In larger gaps created by the windfall of a large canopy tree or groups of trees there is a rapid regeneration response from species with gap-phase replacement. This response involves the development of suppressed seedlings, vegetative reproduction from roots, stumps or fallen stems in the case of kamahi and Quintinia and the establishment of new seedlings. Existing rimu and miro seedlings and saplings can also respond to large canopy openings but are subsequently suppressed by the more rapidly growing gap-phase replacement species. Rata seedlings are sometimes suppressed in the same way. Seedlings and saplings of the shade tolerant species with the continuous mode of replacement do eventually reach the canopy when the initial gap colonisers (predominantly the beech species, kamahi and Quintinia) senesce and die. Canopy tree replacement in large canopy gaps can be viewed as a two stage process with initial colonisation by the fast-growing relatively intolerant species and secondary replacement after a lengthy period (in the order of hundreds of years, see Table 35) by the tolerant species. On this time scale, the regeneration of the shade tolerant species is dependent on the formation of large canopy gaps as with the species with gap-phase replacement.

The effects of natural disturbances are evident today in only small parts of the study area, gales being the most important contemporary agent of disturbance (section 4.13.4). The large-scale regeneration pattern is not therefore an important one in the study area, under natural conditions.

Beech-podocarp forest is more susceptible to windthrow than podocarp-hardwood forest on comparable sites in nearby locations. This appears to result from the greater susceptibility of the Nothofagus species to windthrow compared with the other major canopy tree species. This observation of differing species response to disturbance is relevant to the contention of White (1979) that some kinds of disturbance are initiated or promoted by the biotic community and that, through natural selection, species' regeneration patterns may

be involved in exploiting disturbance.

Primary successions occur to a very limited extent in the study area, being confined to slips in gullies and to flood plains subjected to siltation and water course changes. A secondary succession is in progress on a ridge subject to repeated fires caused by human activity (Appendix V). The species regeneration patterns in this succession are different from those in stands affected by catastrophic natural disturbance. In a situation where all species must regenerate from seed dispersed from adjoining intact forest, rata, miro and rimu in particular are important as initial colonisers during the post-fire succession, and Quintinia and kamahi are not dominant in the early stages of succession. Nothofagus seed sources are not available nearby in this area, but Nothofagus is an important early coloniser of induced secondary successions in places adjoining intact Nothofagus forest. These observations show that in the absence of regeneration from large existing seedling populations and vegetative reproduction, kamahi and Quintinia do not regenerate prolifically and dominate the succession. The other species are able to regenerate prolifically in the open and to grow rapidly, at least in the early stages of the succession. The ability of rimu, rata, miro, red beech and hard beech to act as early colonisers in successions on bare surfaces demonstrates the broad ecological tolerances of these species and an ability to adopt different modes of regeneration in stands subjected to different degrees of disturbance where the competitive interactions of the canopy tree species have been greatly altered.

Results of other New Zealand workers

Supporters of the successional theory of podocarp replacement by hardwood species (Cockayne, 1928; Robbins, 1962) regarded rimu as a light-demanding, pioneering species unable to replace itself in undisturbed mature forest. Robbins (1962) does allow, however, that a few individuals could persist in the hypothetical hardwood-dominated climax community.

The recruitment sequence of rimu in relation to stand composition has been described in some detail in terrace forest in south Westland (Hutchinson, 1928,1932; Poole, 1937; Six Dijkstra, 1981) and in central North Island forests on pumice soils (Beveridge, 1973). The recruitment of rimu occurs by slow development beneath a mature hardwood canopy which has been opened through senescence, windthrow or tree death. In south Westland terrace forests, recruitment also occurs in areas where

the tall forest canopy has been destroyed by windthrow (Hutchinson, 1932). On windthrown areas, which cover from several to 80 hectares, rimu establishes directly on the exposed surfaces and grows to maturity without long periods of suppression from hardwood species.

Veblen and Stewart (1980) described the clustering of rimu and miro seedlings and saplings in large canopy gaps in lowland podocarp-hardwood forest on Bench and Stewart Islands. Miro and rimu appear to regenerate by gap-phase replacement in these forests, sometimes in association with Leptospermum scoparium.

Rata and kamahi share many similarities in regeneration patterns. Wardle (1971 b) referred to the predominantly epiphytic origins of rata seedlings in dense forest and terrestrial origins in light-canopied forests. Kamahi seedlings also establish epiphytically in some forest types (Wardle, 1966; Beveridge, 1973). This mode of establishment is not important in the study area. Holloway (1946) postulated from observations on stand structure an alternation between podocarp and hardwood stands containing rata and kamahi in the Longwood Range. Poole (1937) postulated a similar cycle involving kamahi and Quintinia acutifolia in south Westland terrace forest. This alternation of podocarp and hardwood stages would be similar to the processes described in the study area. Veblen and Stewart (1980) show a dependence on large canopy gaps by rata and kamahi for regeneration in tall forest. Both species function as colonisers in primary successions arising from landslides and glacial activity, being able to colonise bare ground or early stages of succession (Mark et al; 1964; McKelvey, 1955; Cameron, 1960; Wardle, 1966; 1971b; 1980 b). Vegetative reproduction by layering has been observed in rata (Veblen and Stewart, 1980).

Red beech and hard beech are described as light-demanding species with regeneration patterns corresponding to the gap-phase replacement type (Cockayne, 1926; Hocking and Kenderdine, 1945; Kirkland, 1961). Seedlings and saplings present in a suppressed state beneath a closed canopy are observed to respond rapidly by increased growth when the canopy is opened. The large-scale replacement of these species has also been observed in many places (Cockayne, 1926; Morris, 1959; Elder, 1965).

A comparison with northern temperate and tropical forests

In tropical and northern temperate forests tree species can be classified in two categories on the basis of regeneration strategies: early successional species dominant in the early stages, and late

successional species dominant in the late stages of succession and large canopy gap replacement (Ricklefs, 1973).

In the species-rich tropical forests, large numbers of rapidly-growing, shade-intolerant, short-lived tree species with well dispersed seeds are able to colonise large canopy openings or large disturbed areas (Richards, 1952; Budowski, 1970; Whitmore, 1975; Hartshorn, 1978). There is a sequence of species replacement among these early successional species which continues until late successional species become dominant. The late successional species are slow-growing and shade tolerant in the subcanopy stages, have long life spans and produce heavy seeds often with poor dispersal abilities.

The successional sequence in northern temperate forests involves fewer tree species than in the tropics and most of the late successional species are present as suppressed individuals at the beginning of secondary succession (Ricklefs, 1973; Horn, 1974; Borman and Likens, 1979). Both early and late successional species coexist in forest not subject to large-scale disturbance. This coexistence involves the utilization of different reproductive strategies by different species (Forcier, 1975). Early successional species do not regenerate beneath the existing canopy, but disperse widely into large canopy gaps created by the death of canopy trees and subsequently grow rapidly to fill the gap. Late successional species establish and develop at a later stage beneath the canopy of the early successional species. An example is the replacement sequence in gaps: Prunus pensylvanica → Betula spp. → Fagus grandifolia and Acer saccharum (Marks, 1974). Similar examples have been described in north American hardwood forest (Forcier, 1975) and in oak-birch woodlands in northern Britain (Grime, 1979).

A variety of reproductive strategies are employed in regeneration, including a persistent seedling population, vegetative sprouts from roots, stumps and stems and new seedling establishment. Some early successional species rapidly establish in canopy gaps by germination from large numbers of dormant buried seeds which had previously been widely dispersed throughout the stand (Auclair and Cottam, 1971; Marks, 1974). The entry of late successional species into canopy gaps may be delayed and reliant on new seedling establishment (Forcier, 1975; Whitmore, 1975), but in many temperate forests these species develop

largely from existing suppressed seedlings and saplings or from stem and root sprouts (Bormann and Likens, 1979; Grime, 1979).

A comparison of New Zealand forests with northern temperate and tropical forests suggest that exclusively early successional species are rare in the New Zealand tree flora. Leptospermum scoparium, L. ericoides and Cordyline australis are perhaps the only New Zealand trees and small trees in this category, although the Leptospermum species are able to perpetuate themselves in climax communities on extreme sites where tall forest cannot develop (Burrows, 1973).

There is a large group of New Zealand tree species, many of which are important canopy trees in climax forests, which fill the roles of early successional species in successions as well as maintaining themselves in late successional stages. Examples of this group include rimu, rata, kamahi, Agathis australis, Knightia excelsa and Geniostoma ligustrifolium (Dansereau, 1964; Mark et al, 1964; Wardle, 1966; 1971 b; Franklin, 1968). There is in addition a group of shrub and small tree species which are important in early stages of succession but rare or infrequent in climax forest communities. Examples include Olearia rani, Pseudopanax crassifolium, Coprosma lucida, C. robusta and Pittosporum tenuifolium (Cameron, 1960; Silvester, 1964; Esler, 1967). Aristotelia serrata, Carpodetus serratus, Melicytus ramiflorus and Fuchsia excorticata are the most important species in this group in the study stands.

Each of the seven canopy tree species examined in this study is able to colonise bare surfaces and to maintain co-dominance in the later stages of succession. In secondary successions and in replacement in large canopy gaps, the Nothofagus species, kamahi and Quintinia normally fill the role of early gap colonisers and the other species (rimu, rata and miro) achieve co-dominance at a later stage. The growth and reproductive characteristics of each group of species conform to some extent with the contrasting characteristics of early and late successional species recognised in forests overseas, but most of the species do not fit readily into either of the two categories. Rata, for instance, with the shade tolerance and slow growth rates characteristic of late successional species produces small, well-dispersed seeds and can achieve rapid growth to the canopy in some situations. Rimu saplings and poles are also capable of rapid growth in situations where competition from hardwood species is absent.

The species examined in this study, therefore, tend to have broad rather than specific ecological roles. The different regeneration patterns adopted by these species in different competitive situations enable them to function as both colonisers of bare surfaces and as self-perpetuating members of climax communities subject only to canopy gap replacement. This combination of colonising and competitive characteristics may be an important factor in the success of these species as major canopy tree species throughout a wide geographical area in north Westland and elsewhere.

The species with greater competitive ability - Quintinia, kamahi, red beech and hard beech - are generally more successful in colonising new habitats and in replacement in large canopy openings. The other species - rimu, rata and miro - appear to be able to maintain themselves in tall forest vegetation with a strategy of persistence in juvenile and adult stages involving shade tolerance in the subcanopy stages and long life spans. In these respects the two groups of species fall into the categories of 'competitors' and 'stress-tolerators' respectively (c.f. Grime, 1979). The two groups of species, with contrasting regeneration strategies, are able to maintain co-dominance in the same forest communities, albiet with long term fluctuations in the rates of replacement of each species (see section 5.9).

5.8 INTERACTION BETWEEN *NOTHOFAGUS* AND OTHER CANOPY TREE SPECIES

The *Nothofagus* species and other canopy tree species, podocarp and hardwood, coexist in forest communities throughout much of the study area and elsewhere in New Zealand. The long-term nature of this coexistence is evident in the fossil pollen record from Westland and Nelson (section 5.5).

A comparison of the population structures of rimu, rata, miro, *Quintinia* and kamahi in beech-podocarp and podocarp-hardwood forest types on comparable sites (see Table 14) shows that regeneration of these species is continuing in the *Nothofagus* dominant communities. The frequencies of each life stage are generally lower in beech-podocarp forest, but the overall population size structures in the two forest types do not show consistent differences. Canopy tree species which can be overshadowed by the *Nothofagus* canopy, for example kamahi and *Quintinia*, have smaller maximum trunk diameters in beech-podocarp forest (Fig 34). The entry through migration of red beech and hard beech into podocarp-hardwood forest, therefore, results in a reduction in the densities and/or sizes of the podocarp and other hardwood canopy tree species, but not in their elimination from the stand.

Expansion of *Nothofagus* into podocarp-hardwood communities involves the colonisation of canopy gaps by *Nothofagus* seedlings (section 4.6). Podocarp-hardwood forest is not open everywhere to invasion by *Nothofagus*; rather, invasion is dependent on opportunities for successful recruitment to the canopy being created by the formation of canopy gaps. In general only gaps in a narrow band of podocarp-hardwood forest along the margins of *Nothofagus* stands are available for *Nothofagus* colonisation owing to the inefficient dispersal of the genus (section 5.2). Successful colonisation elsewhere is an infrequent occurrence dependent on occasional long-distance dispersal of seed.

As rapidly-growing, light-demanding species, red and hard beech are able to grow towards the canopy in canopy gaps as fast as species with similar regeneration patterns (kamahi, *Quintinia* and rata) and

faster than the shade tolerant species (rimu and miro), section 4.13. Interspecific competition between saplings and poles in large canopy gaps would be intense because of the prolific regeneration of the light-demanding species, but it does not result in the exclusion of the other species from the canopy by red and hard beech (see Table 14).

Following recruitment in canopy gaps, the tall stature, high foliage density and wide lateral branch extension of red and hard beech canopy trees result in interspecific competition in the forest canopy. The extension of the Nothofagus canopy laterally into the canopies of existing rimu and rata trees with the resulting death of the lower parts of the rimu or rata canopy was observed in different places at the Nothofagus boundary in the study area. In one instance, in Stand 4, the presence of a standing dead rimu canopy tree among the canopy of adjoining red beech trees was observed. In this way, interspecific competition for canopy space following invasion by Nothofagus would result in a reduction in the canopy tree densities of other species.

The ability of Quercus petraea trees to suppress adjoining Betula pubescens saplings in oak-birch woods in northern Britain has been related to the greater lateral spread and density of the oak leaf canopy which casts a deeper, more extensive shade than the birch canopy (Grime, 1979). This appears to be similar to the interaction between Nothofagus and other species in the study area.

A reduction in canopy tree density following invasion by Nothofagus will result in a decrease in the numbers of seeds of those species reaching the forest floor because of the reduced density of parent trees. This is reflected in the generally lower rimu and rata seedling densities in beech-podocarp forest compared with similar sites in podocarp-hardwood forest (Table 14). There is some evidence that small seedling survival rates are lower in beech-podocarp forest, although large rimu and rata seedlings have slightly higher survival rates in beech-podocarp forest (section 4.11.4). A lower survival rate of small rimu seedlings could be related to the properties of the surface organic layers in beech-podocarp forest where the fermentation and humus layers tend to be more granular and more liable to drying out on well-drained sites (Mew and Leamy, 1977). Seedling height growth rates are not significantly different in the different forest types (section 4.11.5).

The reduced frequencies of rimu, rata and miro in beech-podocarp forest appear to result, therefore, from direct competition between canopy trees, and possibly between saplings and poles during gap replacement, rather than from competitive inhibition acting at the seedling stage and involving seedling establishment, survival and growth.

5.9 POPULATION STRUCTURES AND PAST REGENERATION RATES

The seven canopy tree species can be divided into two groups on the basis of population size structure characteristics (section 4.10). The overall size structures of hard beech, red beech, Quintinia and kamahi indicate stable, self-perpetuating populations. The stem size-frequency distributions of hard beech, Quintinia and kamahi are clearly J-shaped but the size-frequency distribution of red beech shows a deviation from this form because of a deficiency of smaller trees in the 10 to 60 cm d.b.h. stem size range.

In contrast to the previous group of species, rimu, rata and miro have unbalanced size structures with a deficiency of the smaller size classes from the large seedling to small canopy tree stages. Rata populations generally show greater imbalance than the other species in this group.

The instabilities evident in the population structures of rimu, rata, miro and, to a lesser extent, red beech can be interpreted as resulting from a decline in the regeneration rate within certain periods in the past. Alternative explanations involving episodes of selective mortality among smaller individuals and more rapid growth of smaller trees are not supported by observations of recent mortality and growth rates within the study stands.

There is no evidence of widespread mortality among saplings and poles of these species; deaths occur rarely and do not affect all individuals in a group. In the case of red beech in Stand 5, the widespread mortality following the 1970/71 drought had a selective effect on canopy trees, with most subcanopy individuals surviving this period. In rimu, diameter growth rates are slower in the subcanopy stages than in the larger diameter classes (Fig 35). This is particularly so in the 10 to 30 cm d.b.h. range where the deficiencies in the size-frequency distributions are greatest. Subcanopy individuals of miro and rata are likely to have slow growth rates during suppressed recruitment to the canopy. Red beech saplings and poles would appear to have diameter growth rates as fast as but not faster than growth rates of larger individuals (see Fig 36). This evidence suggests that fluctuations in the rate of population input through seedling establishment, rather than selective, periodic mortality among subcanopy individuals or differential

diameter growth rates throughout the life span are the cause of the unstable population structures.

For the four species with unbalanced population structures, two general changes in future population structures can be predicted. In the immediate future the frequencies of canopy trees will decline as trees die and are replaced by younger members of the population which established during a period of lower regeneration rate in the past. For those populations with relatively high frequencies of individuals less than 10 cm d.b.h. the densities of canopy trees are likely to increase when individuals from the present period of relatively high regeneration rate reach maturity as canopy trees. This is likely to apply particularly to rimu and red beech populations, although the high degree of clumping in red beech saplings may not result in an increased input into the canopy tree stage.

A more detailed analysis is warranted for rimu, for which a reliable age structure for populations on hill slopes is available. An interpretation of the population age structure for rimu (Fig 38) with allowances for mortality loss and growth through the population provides estimates of relative regeneration rates in the past (section 4.10.6). This interpretation suggests that regeneration rates have increased in the past 100 years and are about two to four times the rate for each of the two previous 100 year periods (i.e. 100 to 200, and 200 to 300 years ago). Prior to 300 years ago, regeneration rates were higher than in the past 100 years. Thus, in the 1200 year period covered by the life span of existing trees, regeneration proceeded at a constant and relatively high rate from about 780 A.D. to 1480 A.D. (1200 to 500 years ago), then steadily declined from the period c 1480–1580 A.D. through to the period c 1780–1880 A.D. In the period c 1880 A.D. – present, there appears to have been an upsurge in the regeneration rate but not a return to the level of regeneration pertaining before 1480 A.D. While regeneration has fluctuated markedly with time, there is no evidence for a complete cessation of regeneration at any period during the past 1200 years.

Rimu population structures

The general form of the population size structures in the study area is similar to that found in rimu populations on hill slopes

and terraces in south Westland and Fiordland (Wardle, 1963 b, 1978). Sapling and large seedling frequencies are considerably higher in populations on glacial outwash terraces compared with hill slopes (Wardle, 1978). Similar population structures, i.e. with a deficiency of saplings, poles and small trees, have been observed throughout the country (Table 1).

The variation in size structure on hill slopes in different localities in the study area cannot readily be related to locally variable site or climatic factors. The differences in size structure do not appear to be correlated with differences in the estimated annual rainfall at each locality (Fig 22). Stands similarly deficient in saplings and poles are found, for example, in the 2400-2800 mm isohyet range near Stand 1 and in the 400-4800 mm isohyet range in the Lake Brunner-Rotomanu district. Similar size structures are also found in south Westland (Wardle, 1963 b, 1978) where annual rainfall is generally much higher than in the north Westland study area (Coulter, 1973).

The virtual absence of saplings and poles in the Aorangi Scenic Reserve may be related to the relatively mild, marine-influenced climate of this locality and to the dense ground layer of Freycinetia banksii and other species. Freycinetia is absent from other localities further inland. The soil parent material, marine mudstone, siltstone and sandstone (Table 4), and the soil type (Mew, 1980) are different from the other localities in which observations were made.

The stand with the highest proportion of juveniles, Stand 7 (Fig 29), is located towards the upper altitudinal limit of rimu in the study area. More abundant regeneration at higher altitudes was not generally observed at or near the upper altitudinal limits of rimu in the study area, however. Regeneration in Stand 7 (Lake Hill Ridge) could have been stimulated by the openness of the hardwood canopy. Stand 7 is an exposed ridge-top situation facing the strong south-easterly gales, and the hardwood canopy appears to be more subject to small-scale windthrow than elsewhere.

Within the stands, saplings and poles are found on all types of landform including ridge-tops, upper slopes and lower slopes. Higher densities occur on less well-drained sites of easy slope, such as terraces and some lower slopes (for example Stand 3C).

A comparison of comparable hill sites at Notown (Stand 6) and nearby Lisbon Creek (see Table 4), where regeneration is more abundant, suggests that the observed differences in population structure are related to differences in soil type as determined by parent material and the age of the surface. The floristic composition of the canopy and subcanopy was similar at each locality, except that occasional kahikatea (Podocarpus dacrydioides) was present at Lisbon Creek.

There does not appear to be a correlation between aspect and the amount of regeneration in a stand.

In summary, the differences in rimu population size structure from locality to locality suggest that regeneration is more abundant on less well drained sites, on some soil types (e.g. those derived from calcareous parent materials) and on sites subject to small-scale windthrow.

Miro population structures

The size structure and age-stem size relationship data for miro (Figs 32 and 36) suggest there has been a regeneration decline in this species which parallels the timing and extent of the decline evident in rimu populations.

A regeneration gap in miro has been described by McKelvey (1963) for populations growing on volcanic ash-mantled hill slopes in the west Taupo forests.

Rata population structures

The regeneration failure evident in rata populations (Fig 32) is in some cases more marked than in the rimu population in the same stand. Data of rata tree ages (Fig 36) are inadequate to properly interpret the time course of regeneration failure from the size structures, but the beginning of the regeneration decline appears to date from 200 to 400 years ago. It is possible, therefore, that the decline in rata regeneration began more recently than in rimu. The upsurge in regeneration within the last 100 years evident in some rimu populations has not occurred in the rata populations studied, with the possible exception of the Lake Ridge stand (Stand 7).

Instability in rata populations has been observed elsewhere in the South Island (Wardle, 1971 b).

Red Beech population structures

In the red beech population studied in detail (Stand 5), the beginning of the possible regeneration decline can be dated at between 150 and 200 years ago (corresponding with the 50–60 cm d.b.h. size class, Fig 33). An increase in the rate of regeneration within the past 20 years is suggested by the relative abundance of individuals less than 10 cm d.b.h. (most are saplings less than 5 cm d.b.h.), but the highly clumped dispersion of the saplings means that few will be recruited as canopy trees owing to the high rate of mortality associated with self-thinning in the clumps.

The Stand 5 red beech population is located immediately adjacent to a boundary between beech-podocarp forest and podocarp-hardwood forest. Beech-podocarp forest further removed from the boundary is dominated by hard beech and here, red beech is confined to lower slope and gully sites. The population structure of red beech in Stand 5 could be, at least in part, a consequence of a pioneering origin of the stand which is located adjacent to an expanding beech boundary (see section 4.4). Following a colonisation period in which a moderate density of canopy trees became established, the population appears to be unable to replace itself at the same level. The population may also have been affected by episodes of canopy tree deaths which led to increased regeneration in the period before 150–200 years ago.

Similar population structures and regeneration failures in red beech have been described for hill slope populations in the Ruahine and Huiarau Ranges, North Island (Elder, 1965; June and Ogden, 1978; Grant, 1963), in Southland (Holloway, 1954) and in the Taramakau valley, Westland (Burrows and Greenland, 1979).

Undisturbed red beech populations on flood plains, the preferred site of this species (Table 3), are not now available in the study area. However, red beech populations on lower slopes and alluvial terraces in the Maruia and Reefton districts and other South Island localities are noted for prolific regeneration and apparently stable size structures (Holloway, 1954; Morris, 1959).

Timing of the regeneration decline

The available age structures for rimu show that the onset of the regeneration decline can be dated at between 400 and 500 years ago. The

evidence comes from this study (section 4.10) in which the regeneration decline on hill slopes in north Westland was found to have begun in the period 400–500 years ago, from pumice-filled basins on the Volcanic Plateau where the decline began 400–450 years ago (Herbert, 1980 – Tihoi forest) or 450–500 years ago (Katz, 1980 – Whirinaki forest, Minginui) and on hill slopes in the Longwood Range, Southland where the decline began about 450 years ago (J.A. Bathgate, pers. comm. 1980). Other evidence, which is based on few age estimates, dates the onset of the regeneration failure in rimu at about 650 years ago with an intensification about 350 years ago in a number of South Island localities (Wardle, 1963 b; 1963 c) and at about 400–600 years ago on hill slopes in central Westland (Holloway, 1954, p380).

Age structures have also been obtained for high altitude populations of Libocedrus bidwillii. These show a regeneration decline from about 300–400 years ago in a population on Mt. Pirongia, Waikato (but not in a population on Mt. Te Aroha) (Clayton-Greene, 1977), and from about 280–380 years ago in four stands in central Westland (Norton, 1981). From evidence based on size structures and a limited number of age estimates in other central Westland stands, Wardle (1978) considered that a regeneration failure began about 380 years ago. Interpretation of past regeneration rates is difficult because of the tendency for this species to regenerate in even-aged groups following stand disturbance (Clayton-Greene, 1977; Stewart and Veblen, 1981).

Although age structures have not been derived for red beech, the available size structures and age–size relationships can be used to provide information on the timing of an apparent regneration decline in this species. This can be dated at 150–200 years (this study, Stand 5) and from 140–260 years ago for two mid-altitude stands in the Ruahine Range not obviously affected by past catastrophe (using the data of June and Ogden, 1978).

5.10 POSSIBLE CAUSES OF THE 'REGENERATION GAP' IN RIMU AND OTHER CANOPY TREE SPECIES.

For the three species with marked 'regeneration gaps' (rimu, miro and rata) the following generalisations can be made (refer sections 5.6, 5.7 and 5.9):

(i) the regeneration failures are a feature of populations throughout wide areas;

(ii) the regeneration failures appear to be synchronous for each species over wide areas and on different sites;

(iii) there is some evidence that past regeneration failures in different species do not coincide (a failure in rimu and miro apparently began before a failure in rata);

(iv) the degree of regeneration failure varies from site to site;

(v) the regeneration of rimu is more abundant on poorly-drained terraces than on hill slopes and also on soils derived from calcareous parent materials.

(vi) the species have predominantly (rimu and miro) or secondary (rata) continuous regeneration patterns;

(vii) the rate of recruitment to the canopy is limited by competition in canopy gaps from the major hardwood species (red beech, hard beech, kamahi and Quintinia);

(viii) Canopy disturbance of a minor nature may increase the rate of regeneration of rimu and miro;

(ix) the species have low seedling densities;

(x) rimu and, in particular, rata have specific microsite requirements for early establishment and miro has broad microsite requirements;

(xi) the availability of suitable microsites for early seedling establishment does not appear to be a factor limiting the rate of regeneration throughout most stands (rata may be the exception, however);

(xii) the species are shade tolerant in the subcanopy stages, however, rata is less tolerant than rimu or miro;

(xiii) the seedlings do not develop and survive where there is a dense shrub or ground layer (as in large canopy gaps).

For red beech there were fewer observations of undisturbed stands to draw on, particularly for stands on alluvial sites. A partial regeneration failure for this species is evident in the hill slope stands examined and appears to have begun more recently than in rimu, miro and rata.

There are a number of stages in the life cycles of canopy trees where a regeneration failure could occur. These include seed production and dispersal, germination, seedling establishment, and recruitment to the canopy. During each stage individuals are subject to a continual mortality risk as a result of pathogen attack, browsing, desiccation, etc. They are also vulnerable to intra- and inter-specific competition from other plants. The initial imput into the population is determined by numbers of viable seed reaching the ground, the survival rate of seed through the overwintering period and the germination rate. Suitable microsites on the forest floor must be available for seed survival, germination

and early seedling survival. For species with specific requirements the availability of favourable microsites could be a limiting factor.

While microsite availability does not appear to limit the early establishment rates of rimu, rata and miro (section 5.6), the further development and survival of seedlings of these species is limited by competition from hardwood species in large canopy gaps. The seedlings establish in many microsites where their further development is inhibited. Rimu, rata and miro have low to very low seedling densities and low rates of early establishment compared with the other species studied. Red beech, in which a partial regeneration failure is evident, has lower seedling densities and establishment rates than hard beech, kamahi and Quintinia, the species with stable population structures. Red beech and rata share the light-demanding and fast-growing characteristics of this group of species in the sapling and pole stages. These considerations together suggest that the factors causing a regeneration decline in rimu, rata, miro and red beech are likely to be effective largely in the early stages of the life cycle, from seed production to the early stages of seedling establishment.

The requirements for seedling establishment would be consistent with climatic factors such as insolation and effective precipitation influencing the rates of seedling establishment. Desiccation is likely to be a major cause of mortality for seedlings which germinate on litter, and may also be an important cause of mortality for older seedlings, particularly those located in exposed microsites in canopy gaps. Desiccation would be more prevalent during long periods when rainfall was deficient, particularly during the

warmer seasons. Periods of up to three weeks without rainfall were observed during the spring and summer in the study area. During these periods the litter and upper humus layers of the forest floor became very dry and the mortality of small seedlings and wilting of small shrubs became apparent. The more abundant regeneration of rimu on poorly-drained sites and the microsite preferences of large rimu seedlings could be a result of a more favourable soil moisture regime on these sites and microsites, although it is possible that the more abundant regeneration is such places is related to other soil factors such as nutrient availability or the unfavourability of these sites and microsites for competing species. Regeneration of rimu is not more abundant in parts of the study area which receive higher annual rainfall. This lack of response to a rainfall gradient suggests that precipitation may not be an important limiting factor for seedling establishment.

The amount of light reaching the forest floor may affect seedling growth and survival when seedlings are growing in microsites at or near their light compensation points. This factor would be more important for rata seedlings which are less shade tolerant than rimu or miro seedlings. The amount of light reaching seedling microsites would be a function of the amount of sunlight incident on the forest canopy and the shading effect of canopy, subcanopy and ground foliage layers. It is possible, therefore, that the vigour of the major hardwood tree species (in terms of their density in canopy, subcanopy and ground layers and ability to rapidly infill canopy gaps) could affect the survival of miro, rata and rimu seedlings through their influence

on the light regime on the forest floor. Root competition from hardwood canopy trees could also be involved in controlling the regeneration of these species.

An evaluation of the hypotheses advanced to explain the 'regeneration gap'

Five major hypotheses have been advanced to explain the 'regeneration gap' in New Zealand gymnosperms. These involve long-term successional trends, cyclical regeneration patterns, catastrophe-dependent regeneration, biotic changes and climatic changes. The relevance of each hypothesis in explaining the 'regeneration gap' of rimu, miro, red beech and rata in the study area is examined in turn.

Successional trends

Cockayne (1928) considered the podocarp species to be a declining element of existing podocarp-hardwood forests. He characterised the podocarps as light-demanding members of early successional stages in forest development which were being replaced by the shade-tolerant or shade-demanding hardwood species such as tawa (Beilschmiedia tawa) and kamahi (Weinmannia racemosa). The hardwood species would form the eventual climax community with the podocarp species rare or absent. These ideas were elaborated by Robbins (1962) using a geological time scale as a perspective for the competitive interaction of the gymnosperm and angiosperm elements of mixed forests. Wardle (1963b, 1973a) has discussed the limited applicability of this concept to the phenomenon of a recent regeneration

decline. The post-glacial fossil record (e.g. Moar, 1971) demonstrates in many localities long periods of coexistence of gymnosperm and angiosperm elements in forest communities.

One such example is of a rimu dominated forest present continuously for the postglacial forest phase at Bell Hill, in the study area (Moar, 1971).

Regeneration cycles

In many forest communities podocarps appear to regenerate beneath the mature and senescent hardwood stand components which had previously colonised gaps formed by the death of podocarp trees. Podocarp regeneration is seen to occur as part of a small-scale, cyclical succession with alternating podocarp-dominant and hardwood-dominant phases (Hutchinson, 1932; Poole, 1937; Cameron, 1954; Beveridge, 1973). In a stable community, all stages of the regeneration cycle should be present in a mosiac pattern throughout the stand. However, it is observed that the young podocarp replacement stages in the regeneration cycle may be absent over wide areas (J.T. Holloway in a comment appended to Cameron, 1954 (N.Z. Journal of Forestry 7: 65-7)).

There is no evidence in the study area of synchronised regeneration cycles in which the podocarp species or rata are absent for part of a regeneration sequence over wide areas. Regeneration cycles do, however, operate on the level of individual canopy tree replacement. The existence of a regeneration cycle involving podocarp and hardwood phases does not therefore explain the 'regeneration gap'.

Catastrophe-dependent regeneration

Periodic, catastrophic destruction of forest stands has been suggested as a pre-requisite for the regeneration of podocarp species (Molloy, 1969). A study of Libocedrus bidwillii indicated that separate stands in the same locality became established at different periods in the past 500 years (Clayton-Greene, 1977). Gales and landslips were considered to be the agents which stimulated regeneration of the stands. This regeneration mechanism would not appear to be operative over large areas of forest where there is no evidence of large-scale, catastrophic disturbance of the forest canopy within the life span of existing trees.

Canopy trees of the three species showing a marked regeneration decline in the study area do not appear to be commonly affected by natural catastrophic damage. On hill slopes, canopy trees of each species are relatively windfirm and drought tolerant compared with the main hardwood canopy tree species on the same sites. There is no evidence of episodes of widespread large seedling, sapling or pole mortality in rimu, miro and rata.

It has been suggested that violent storms resulting in large-scale windthrow may have stimulated

podocarp regeneration prior to the period of regeneration failure when comparative calm prevailed (Wardle, 1979). There are several objections to this possibility. Widespread windthrow affecting rimu, miro and rata does not appear to have occurred in the recent period when there has been a upsurge in regeneration in some parts of the study area, at least for rimu. Catastrophic windthrow does not affect all sites equally over a wide area; sheltered stands in valleys and on lee slopes often escape damage. The historical pattern of windthrow events is not therefore a likely explanation for the 'regeneration gap' which is a common feature on a range of sites over a wide area. A further consideration is that the prolific regeneration response of the hardwood canopy species to windthrow and other large-scale disturbance of the canopy is likely to suppress rather than stimulate the recruitment of rimu and miro, although rata regeneration would probably increase.

This gives rise to the possibility that rimu and miro regeneration may have been more abundant during periods of relative calm when there was less disturbance of the hardwood canopy, enabling the podocarps to take advantage of small canopy gaps in a relatively stable canopy and to avoid the competitive exclusion due to dense hardwood regrowth in large canopy gaps. This mechanism entails small differences in the abilities of the podocarp and hardwood species to exploit canopy openings of different size and frequency. Thus, rimu and miro with continuous regeneration modes (section 5.7) would be able to respond to small, temporary canopy openings by increased establishment rates, but the less shade

tolerant hardwood species would be less able to respond to these openings.

The population structures of rata may reflect a different response to canopy disturbance compared with the podocarp species. An upsurge in rata regeneration following massive canopy disturbance could have coincided with the beginning of the period of podocarp regeneration decline, and the formation of relatively dense stands of rata trees may have had a continuing suppressing effect on further podocarp recruitment (as well as a self-suppression effect). Red beech populations may have responded in a similar way.

On the basis of the present evidence it is postulated that the rate of podocarp regeneration is controlled indirectly by long-term environmental changes through the mortality and regeneration responses of the hardwood canopy tree species.

An event or series of events which severely damaged the hardwood canopy (but which did not cause the deaths of existing rimu, rata and miro canopy trees) could have led to an upsurge of hardwood regeneration in the open stand conditions thereby created. This would involve an upsurge of rata and possibly red beech regeneration as well as Quintinia, kamahi and hard beech regeneration. Shrub species such as Carpodetus serratus and Aristotelia serrata could also have regenerated prolifically. During this period, rimu and miro regeneration would have been suppressed by the dense regrowth of the hardwood species, and then subsequently by the dense hardwood canopy that had arisen. During this latter period, the regeneration of rata and possibly red beech would be inhibited by the canopy conditions. At a later

period still as the mature hardwood canopy became subject to thinning through senescence and mortality, conditions would again become more favourable for rimu and miro regeneration although not for rata regeneration. Thus, a sequence of continuing changes in the population structures of the canopy tree species, involving regeneration failures at different periods in at least some of the species, could be initiated by a large-scale disturbance of the hardwood canopy.

The period in which this postulated disturbance occurred can be tentatively derived from the available information on population structures (section 5.9). The disturbance would have occurred between about 400-500 years ago (the period in which a regeneration decline in rimu began in different localities) and 150-400 years ago (the period in which rata, Libocedrus bidwillii and possibly red beech regeneration began to fail). A disturbance involving the windthrow of clumps of hardwood trees would also be likely to cause the windthrow and death of rimu and miro poles present in the stands. This would have the effect of making the regeneration decline in rimu and miro effective to a time before the period of the disturbance. On the other hand, large seedlings and saplings of rimu and miro may have been able to survive a disturbance of this nature and to be recruited to the canopy in the open conditions subsequently prevailing (before hardwood regrowth prevented further podocarp seedling establishment). The earlier acceleration of diameter growth in rimu trees older than 300 years (Fig.45) may have been a response to these conditions.

Large areas of podocarp-hardwood forest, in which all hardwood canopy trees have died within a relatively short period leaving rimu canopy trees standing above low, dense hardwood regrowth, are present in Erua State Forest, Central North Island (personal observations, 1977). Kamahi and Carpodetus serratus are the most important species in the regenerating hardwood shrub layer. This stand structure is similar to that which would develop immediately after the postulated large-scale destruction of the hardwood canopy.

There are a number of destructive events other than storms which could have affected the hardwood canopy. Tree mortality caused by droughts or pathogen attacks, or canopy damage caused by heavy snowfalls could occur over large areas of forest. These events may have a less localised effect than wind storms.

Biotic changes

The arrival of man in New Zealand has resulted in significant changes in the forest fauna during the past 1000 years with the introduction of exotic species and the extinction of some indigenous bird species. Introduced animals, particularly rodents, possums and ungulates, have had a considerable adverse impact on forest regeneration by seed and seedling predation, foliage browsing, bark rubbing and trampling of the forest floor (McKelvey, 1959; Beveridge, 1964; Gibb and Flux, 1973).

Introduced rodents, which consume significant quantities of podocarp seeds (Beveridge, 1964; Herbert, 1978), would cause losses of seed on the forest floor in addition to predation losses from indigenous

insects and thereby have an adverse effect on regeneration. The periodic seeding behaviour of the podocarp and beech species may mean, however, that animal populations are unable to exert severe predation on seeds during mast seed falls (Beveridge, 1964; Ogden, 1971). Prolific podocarp regeneration did occur in Pureora forest following heavy seed falls, despite seed predation by rodents (Beveridge, 1964). The proportion of viable seeds destroyed by the rodents has not been assessed. Rodent predation of rata seed would not be significant because of the small seed size (less than 0.1 mg, Wardle, 1971b). Where high populations of rats are present, podocarp seedlings can also be eaten (Beveridge and Daniel, 1965). Browsing of seedlings by goats and in some places by deer can be severe (Beveridge, 1964; Franklin, 1968). Podocarp seedlings are, however, relatively unpalatable to browsing animals (Wardle, 1974) and may be favoured by heavy browsing of the competing hardwood under-storey (Holloway, 1950).

Substantial changes have occurred in the forest floor bird fauna in the past 1000 years. The loss of foliage-eating birds such as the kakapo (Strigops habroptilus) and the moa (Ratite) group may have resulted in a reduction in browsing pressure on palatable ground and shrub layer plants (Greenwood and Atkinson, 1977). Understorey and canopy species could then have increased in abundance and size, leading to increased suppression of podocarp and rata seedlings. The exotic ungulates introduced into the study area during the past 80 years may have had a similar effect to that of the extinct bird fauna in reducing competing species and this could be associated with an upsurge in

regeneration during this period in some localities.

There are several limitations to the postulated association between the presence or absence of understorey browsing animals and fluctuations in the regeneration rates of canopy tree species. To cause a severe inhibition in the rate of regeneration (in some stands amounting to a nearly complete failure of regeneration over hundreds of years) the browing pressure on competing understorey species at other periods would need to have been continuous, intense and effective over wide areas. The major plant species inhibiting podocarp and rata regeneration in the study area are not very palatable to introduced ungulates (Wardle, 1974) and the abundance and fast-growing nature of their seedlings and vegetative shoots would mean that intense browsing pressure would be needed to suppress their regeneration.

The paucity of dated fossil records for earlier bird faunas and the lack of information on the browsing habits of extinct species in the forest types found in the study area make further consideration of this hypothesis difficult.

The possibility of introductions of bacterial, fungal or insect pathogens by man, and widespread epidemics of indigenous pathogens must also be considered as potentially damaging agents of the forest canopy in the past.

Climatic change

A deterioration in regional climate is the most widely accepted explanation for the 'regeneration gap'. Acceptance of this hypothesis is based on the apparent

synchroneity of the regeneration failure over a wide area of New Zealand in forests unaffected by large-scale disturbance and growing on a range of sites. Other, apparently coincident vegetation changes indicative of climatic changes have also been described. Examples include the lowering of tree altitudinal limits (McKelvey, 1963) and the migration of Nothofagus species (Holloway, 1954). The range expansions of Nothofagus are now seen as a continuing postglacial trend rather than solely as a response to recent climatic change (Wardle, 1973a).

Possible causal factors of the regeneration failure include a decrease in temperature accompanied by a decrease in rainfall (Holloway, 1954; Wardle, 1963b, 1978) a reduced incidence of canopy-damaging gales (Wardle, 1979), a decline in insolation associated with increased storminess (Wardle, 1973b) and occurence of drought (Burrows and Greenland, 1979). These causal factors have been suggested from observations on the distribution patterns and seedling microsite preferences of species exhibiting the 'regeneration gap'. Direct evidence of the effects of long-term climatic fluctuations in seedling establishment and recruitment is lacking.

Continuous records of climatic changes as they affected natural phenomena during the past 1000 years have been derived from evidence of glacial advances, erosion and aggradation rates (reviewed by Burrows and Greenland, (1979), oxygen isotope ratios in speleothems (Wilson et al., 1979) and carbon isotope ratios in the wood of long-lived trees (Grinsted and Wilson, 1979)

There is an overall correlation between the beginning of the period of regeneration decline and a series of glacial advances since c 1600 A.D., as noted by Wardle (1963b). The period of regeneration decline

for rimu also follows the general, decreasing trend of palaeotemperature since c 1400 A.D. (Wilson et al., 1979) but with a lag period of about 100 years. This general agreement between inferred regeneration rates and the climatic record does not hold in some points of detail, however. Glacial advances in the Mount Cook region began c 1000 A.D. and occurred in nearly every century from then until the 19th Century. There is no indication from the available data that any were more or less severe than others (Burrows, 1982). Inferred temperature minima at c 1450 A.D. (Wilson et al., 1979) and c 1290-1070 A.D. (Grinsted and Wilson, 1979) predate the beginning of the period of regeneration decline. During the period of maximum rimu regeneration decline from 1600A.D. to 1850 A.D. (Wardle, 1963b; this study) two relatively warm periods occurred at about 1700 A.D. and 1800 A.D. but did not result in an increase in regeneration. The pattern of a steadily declining rate of regeneration through the period from 1480-1580 A.D. to 1780-1880 A.D. when a minimum rate of regeneration was reached (section 5.9), does not appear to be paralleled by any clear trends in the climatic record. However, the post-1850 A.D. regeneration upsurge is associated with a temperature increase in the palaeo-temperature record (Wilson et al., 1979), a temperature rise from c 1900 A.D. to the 1960's (evident in meteorological records), and glacier recession and rising snowlines in the same period (Burrows and Greenland, 1979).

The climatic record for changes in precipitation throughout the past 1000 years is an inadequate one. There is, however, evidence for low water levels in

closed basin central North Island lakes in the 17th and 18th centuries and about 1890 A.D. (Burrows and Greenland, 1979). This evidence indicates low precipitation in this region during these periods. The poor correlation between Westland and the North Island in recent rainfall records (Trenberth, 1977) makes extrapolation of the lake level records to Westland unreliable. There is, in addition, indirect evidence which suggests that precipitation in Westland was higher during the glacial advances of the 17th and 18th centuries. This is based on a positive correlation between advances of the Franz Josef glacier in the past 90 years and the annual rainfall recorded at Hokitika (Suggate, 1950). There is some uncertainty, however, whether glacial advances are directly associated with increased precipitation (Burrows and Greenland, 1979), so this correlation may not hold over a long time scale and for the major glacial advances of the past 1000 years. The possibility that the regeneration decline resulted from decreased precipitation cannot, therefore, be ruled out on the basis of present knowledge.

Increased storminess, possibly with associated heavy rainfall and resulting in erosion and shingle deposition in river valleys, is postulated to have occurred since about 1650 A.D. in the North Island (Grant, 1963; 1965; Pullar, 1970). Human and tectonic activity could be a factor in the increased erosion and deposition rates. As suggested previously, increased storminess which resulted in increased damage to forests during this period could lead to a decline in regeneration rates.

The lack of close correlation in the timing of known climatic changes and regeneration rates may result

from an indirect causal relationship, for example when one species responds to a climatic change by increased regeneration and, throughout its life span, suppresses another species regardless of subsequent climatic changes. This type of interaction could also account for a lag period between climatic trends and the onset of a regeneration decline.

Overseas work on regeneration failure

"Regeneration gaps' have been noted in tropical and northern temperate forest species (e.g. Whitmore, 1975; Harcombe and Marks, 1978) and a variety of explanations, including climatic change, have been proposed. Whitmore (1974) has associated population structures deficient in younger individuals with the ecological strategies of light-demanding species where recruitment is largely confined to canopy gaps. He does not consider population structures of this nature to be unstable. Harcombe and Marks (1978), in discussing possible causes for the underrepresentation of subcanopy individuals in populations of dominant tree species in Southeast Texas, considered that periodic seed production, past logging and regional climatic changes were contributing factors, but that mortality caused by competition from canopy trees and the understorey was the major cause.

Unstable population structures with even-aged groupings of individuals which established at different periods are found in a number of temperate tree species (Jones, 1945; Alder and Harper, 1969; Miller, 1970; Leak, 1975; Oliver and Stephens, 1977; Lorimer, 1980; Veblen et al., 1980). These species are found in forests prone to catastrophic disturbances caused by gales, landslides, volcanic eruptions, logging and diseases. Their population structures reflect a regeneration response to periodic large-scale destruction of the canopy.

Changes in regional climates do not appear to have been postulated elsewhere as a major cause of changes in regeneration rate over the past 500-1000 years. This may be in part a consequence of the catastrophe-prone nature of many temperate forests where the regeneration responses following catastrophe would obscure long-term regeneration trends and where trees do not attain long life spans. In tropical forests there is a dearth of data on tree ages because of difficulties in ageing trees (Sarukhan, 1980). Successional trends can also obscure interpretation of long-term environmental changes.

A population age structure for one long-lived North American tree, Sequoia sempervirens, shows some deficiencies in the frequencies of the 200-300, 300-400, and 400-500 year age classes compared with a stable distribution (Fritz, 1929; Namkoong and Roberds, 1974). The authors did not consider the population structure to be unbalanced. This species is subject to episodes of widespread mortality through fire and siltation, which may be responsible for the anomalies noted above.

In some studies (e.g. Whitmore, 1974; Veblen and Stewart, 1980), population structures obtained from sample plots are interpreted without reference to the whole population. Deficiencies in younger age classes are attributed to the regeneration pattern of the species concerned. For long-lived species with gap-phase replacement, the scale of sampling will be important in determining the population structure obtained. Small sample plots may show deficiencies in certain size/age classes, whereas larger sample plots

or combined data from small plots may show balanced population structures. Interpretation of population structures in this way is not satisfactory for the species examined in this study where age class deficiencies are a consistent feature of some populations over large areas.

CHAPTER SIX
GENERAL SUMMARY

The ecotone between the beech-podocarp and podocarp-hardwood forests of north Westland borders one of the major anomalous discontinuities of Nothogagus distribution in New Zealand. Observations made along this ecotone and in the adjoining areas show that the Nothofagus species are expanding their range along much of the ecotone and have the potential to migrate further southwards into central Westland onto most growing sites between sea level and timberline.

The slow migration rates of Nothofagus species described by other workers (eg. Holloway, 1954; Preest, 1963, Wardle, 1970b) are generally confirmed by this study. Migration is largely confined to slow spread along the margins of existing stands following seedling establishment in canopy openings in podocarp-hardwood forest or on bare sites immediately adjacent to the stand margins. Nothofagus seedlings are rarely found more than 20m from the trunks of beech trees forming the boundary of a stand. The role of water dispersal in effecting relatively rapid downstream migration is evident in north Westland, but does not appear to be as important as described by Holloway (1954) in the forests of western Southland. Migration is relatively rapid along river valleys in both upstream and downstream directions, and also on poorly-drained glacial outwash terraces and the upper slopes of the southern Paparoa Range. The availability of newly-exposed surfaces and the presence of open-canopied vegetation of low stature may facilitate more rapid migration on these sites. Long distance dispersal across dry land with a maximum range

of 4-6 km resulting in the establishment of new outliers has previously been inferred (Burrows, 1977; Wardle, 1979). In North Westland, outliers up to 12 km from the nearest potential parent stands appear to have arisen following seed dispersal over this distance. The general dispersion patterns of outliers, which are located mostly close to the main beech forest boundary, are consistent with the infrequent dispersal of seed by wind away from parent stands. Although long distance dispersal can lead to the establishment of new colonies at great distances from existing stands, the contribution of this mode of dispersal to the overall expansion of range is not a large one, except in upland sites in the southern Paparoa range where outlier formation is more frequent than in the lowlands.

A requirement for mycorrhizal associations may limit the establishment of Nothofagus seedlings beyond the rhizosphere of existing Nothofagus trees, particularly in soils with low phosphorus status. This requirement appears to be a limiting factor in long distance dispersal, although the results of various investigations into seedling establishment and nutrition and the presence of mycorrhizae in stands likely to have originated following long distance seed dispersal provide some conflicting evidence on the role of mycorrhizae. Further investigation on seedling establishment in the field is required to clarify this role.

An earlier view of the impact of Pleistocene glaciation on vegetation (Willett, 1950) held that forest vegetation would have been confined to refugia in the north-western and northernextremities of the South Island during the Otiran glaciation. The present study provides evidence for a much wider distribution

of glacial period refugia, including refugia close to Otiran ice limits. The slow migration of the Nothofagus species evident in the present day forests means that postglacial dispersal to the present distribution limits would not have been possible from more distant refugia. The Nothofagus species distributions in north Westland, given the slow rates of migration, point to the location of at least two glacial period refugia. These are found at Blackwater Creek near Kumara and in the Runanga district. A further seven local refugia within the study area are proposed on less substantial distributional grounds (including a consideration of likely past migration routes derived from the present distributions of the four species in relation to the local topographical and drainage patterns).

A wider distribution of vegetation refugia in the South Island than that proposed by Willett (1950) has also been suggested by a number of authors on the basis of the early appearance of Nothofagus in the Aranuian fossil pollen record at different places including north Westland (e.g. Moar and Suggate, 1973; Lintott and Burrows, 1973; Wardle and McKellar, 1978). The results of the present study, using different evidence, confirm this picture. At the sametime it appears that the rate and extent of postglacial expansion for Nothofagus would have been several times greater outside the north Westland study area, at least in the montane valleys of the Southern Alps. This more rapid migration could be a consequence of the more unstable geomorphic environment in these valleys and the presence of low, open-canopied vegetation which is more susceptible to invasion by Nothofagus.

The localised distributions of some animal species has also led to the proposal of a number of glacial vegetation refugia in Westland and other regions of the South Island (Forster, 1954; Lee, 1959; Climo, 1975). Actual refugia locations were not proposed by these authors. The distribution patterns of animal groups such as the Paryphantidae with locally endemic species in Westland may be a means of testing the likelihood of the nine proposed refugia. Further information would be required on the distributions of these species.

The presence of a 'regeneration gap' is confirmed in rimu and miro populations in north Westland. A 'regeneration gap' is also present in southern rata populations, where it is more pronounced than in the podocarp species, and to a lesser extent in red beech populations. The absence or infrequency of seedlings, saplings and poles in these species is a widespread feature within the study area, although there are some variations in population structure from place to place. The 'regeneration gap' cannot be explained in terms of differential growth or mortality rates in different stages of the population or as a consequence of a particular mode of regeneration as suggested by other authors (e.g. Harcombe and Marks, 1978; Veblen and Stewart, 1980).

In the rimu populations studied, the beginning of a past decline in the rate of regeneration can be dated to the period 400-500 years ago. This is in agreement with the estimates derived from rimu age structures which have recently been obtained in other regions (J.A. Bathgate, pers. comm. 1980; Herbert, 1980; Katz, 1980). A more detailed interpretation of past regeneration rates is attempted, using the age structure and estimates of growth and mortality rates

obtained from study stands. For the period covered by the lifespans of existing trees (up to 1200 years), the regeneration rate appears to have been constant up to about 500 years ago and then to have declined steadily through to the period 100-200 years ago. In the past 100 years there has been an increase in the regeneration rate.

Past fluctuations in the regeneration rates of southern rata, red beech (this study) and Libocedrus bidwillii (Wardle, 1978; Norton, 1981) do not coincide with those apparent in rimu. A regeneration decline in these species appears to have begun at a later date, within the period 150-400 years ago.

A comparison of the regeneration characteristics of the major canopy tree species studied suggests possible ways in which the rate of regeneration is controlled. Rimu and miro have the continuous mode of regeneration, are shade tolerant and have long recruitment periods. Southern rata and red beech are more light-demanding, have shorter recruitment periods and have the gap-phase mode of regeneration as a primary mechanism. Rata does, however, share some of the characteristics of rimu and miro, including narrow microsite requirements for seedling establishment and a high shade tolerance. Red beech is a light-demanding species which otherwise has a regeneration pattern similar to that of Quintinia, kamahi and hard beech, species which do not exhibit 'regeneration gaps'. Of this group of species red beech has the lowest seedling population densities indicating lower rates of seedling establishment. Seedling establishment appears to be the stage at which a regeneration failure occurs. Many favourable microsites lack seedlings of the species

concerned, and in some microsites seedlings fail to develop past the small seedling stage largely because of competition from dense thickets of hardwood saplings which rapidly develop in newly formed canopy gaps. The competition from the hardwood gap colonisers appears to be a major factor controlling the regeneration of rimu, miro and southern rata.

It is proposed that past changes in the regeneration rates of rimu, miro, southern rata and red beech result from the differing responses of these species to a catastrophic opening of the hardwood canopy at some time during the period from about 300 to 500 years ago. Severe and extensive damage to the hardwood canopy during this period could have led to an upsurge in hardwood regeneration, including southern rata and red beech regeneration. The dense regrowth of the hardwood species and the dense canopy subsequently formed would have had the effect of suppressing rimu and miro regeneration over the following several hundred years. Further regeneration of southern rata and red beech was also inhibited. In this way the contrasting regeneration characteristics of each species, including the responses to canopy opening, result in regeneration declines at different periods.

A number of explanations of the 'regeneration gap' phenomenon have been offered. Most are concerned with the role of past changes in regional climate and the forest fauna and the periodic, catastrophic destruction of forest stands (Molloy, 1969; Burrows and Greenland, 1979; Wardle, 1979). It is possible that an increased incidence of drought, the introduction of seed eating rats, the extinction of understory browsing animals and widespread canopy destruction caused by gales, snow falls

or pathogen attack may have been involved.

An important difficulty with each explanation is the need to account for the apparent synchroneity of the 'regeneration gap' in different groups of species at different times over much of New Zealand. For species with wide ecological and climatic amplitudes the relatively minor climate changes inferred for the past 1000 years would seem to be unlikely to cause an almost complete cessation of regeneration. Climatic changes within the past 1000 years in New Zealand show major regional differenees (Burrows and Greenland, 1979). The spread of introduced species and the extinction of indigenous species as a result of the activities of Polynesian man could have occurred within a relatively short period throughout the country. Canopy destruction caused by gales, snowfalls and other agencies is observed to be localised in extent, although it is possible that a pathogen epidemic affecting the major hardwood canopy tree species could have spread rapidly over wide areas. The lack of reliable information on changes in the physical and biotic environment throughout the past 1000 years makes it difficult to evaluate the various hypotheses that have been proposed to explain the 'regeneration gap'. This situation is, however, improving with continuing research on climatic and biotic history.

The anomalous features of the north Westland forest vegetation which are the subject of this thesis were earlier considered to be a consequence of the same historical event; a deterioration in regional climate involving a decrease in temperature and rainfall beginning about 800 years ago (Holloway, 1954). From the results of the present study and other investigations (e.g. Wardle, 1963b; Moar, 1971; Russell, 1980) it is

now evident that these anolmalous features represent responses of the plant species to different environmental changes which were effective over greatly different time scales.

The present distributions and migratory behaviour of the Nothofagus species in north Westland provide evidence that the genus is still spreading into its potential range in Central Westland from refugia positions dating from the last glacial period. This expansion of range has apparently continued throughout the forest phase of the postglacial, a period covering the last 9000 to 12000 years (Moar, 1971; Moar and Suggate, 1979) and followed a major climatic shift to warmer, more equable conditions.

On a contrasting time scale, the population structures of rimu, miro, southern rata and red beech show evidence of continuing responses to environmental changes within the past 500 years. These responses, which post-date the changes postulated by Holloway (1954), cannot be unequivocally attributed to a general decline in rainfall and temperature. It is likely, for instance, that biotic changes associated with the colonisation of New Zealand by man and the incidence of past canopy damaging events such as gales and snowstorms are implicated in the regeneration declines. The Holloway hypothesis cannot be sustained in its enirety, therefore, but the phenomena of the 'regeneration gap' of podocarp species and the continuing migration of Nothofagus documented by Holloway are important features of the north Westland forests and will continue to have a profound influence on community and population structure throughout that region.

CHAPTER SEVEN

SUMMARY OF CONCLUSIONS

1. The four Nothofagus species reach southern limits of distribution in north Westland between Greymouth and Harper's Pass. The distributions of the three species of the fuscoid group are similar whereas N. menziesii has a more restricted distribution in the lowlands and a wider distribution in the Paparoa Range. Nearly all growing sites from timberline to sea level within the area of distribution are occupied by one or more of the Nothofagus species which form a nearly continuous forest canopy over wide areas.

2. Enclaves of podocarp-hardwood forest ranging in size from 0.4 ha to 4500 ha occur within the main area of Nothofagus distribution. These enclaves are formed as a result of the more rapid expansion of Nothofagus along valley bottoms, high outwash terraces and upland slopes compared with other sites.

3. Nothofagus outliers ranging from single individuals to stands 360 ha in size are found up to 16 km from the main area of distribution. Outliers are more frequent in the upland zone of the southern Paparoa Range than in the lowlands. The frequency of outliers declines exponentially with increasing distance from the presumed parent stand. Most outliers appear to establish following the dispersal of seed away from parent trees over

distances of up to 12 km. One outlier, at Blackwater Creek near Kumara, has features consistent with a relict origin from a more widespread, pre-Otiran distribution.

4. The boundary between Nothofagus-dominant and adjoining communities is abrupt and in most areas shows evidence of an expansion in the Nothofagus range.

5. The position of the Nothofagus boundary in north Westland cannot be correlated with known regional patterns of variation of soils or climate, although there is some evidence that the boundary is associated with a regional floristic boundary. There appear to be no climatic, soil or site barriers to a further extension of range southward into central Westland.

6. The expansion of Nothofagus into a podocarp-hardwood forest community results in a reduction in the density and maximum stem diameters of other tree species.

7. Nothofagus seedlings established from seed sown experimentally in a podocarp-hardwood forest showed little or no height growth over three years and lacked the normal mycorrhizae. The difficulty in forming an effective mycorrhizal association following seedling establishment beyond the rooting zone of parent trees may limit the rate of migration. The limited range of seed dispersal under normal conditions and the availability of canopy openings in existing vegetation also contribute to a slow rate of migration.

8. Estimates of migration rates derived from population age structures at the existing Nothofagus boundary show an extremely slow rate of migration (about 0.1 m/yr) into stable vegetation on hill slopes by marginal spread. Migration by marginal spread is slowest on hill slopes and more rapid on poorly-drained outwash terraces and on flood plains. Downstream migration along flood plains is more rapid than upstream migration, presumably because of the long-distance dispersal of water-borne seed during floods.

9. The contribution of outlier establishment and espansion to the overall rate of migration is limited, except in the upland zone of the southern Paparoa Range where there is more frequent outlier formation.

10. The fossil record for north Westland does not show clear evidence for climatic control of Nothofagus spread during the postglacial. The fossil record would be consistent with either slow expansion from local refugia or rapid migration from distant refugia.

11. Nine, widely distributed glacial period Nothofagus refugia at coastal and inland locations in the lower and middle sections of the Grey-Inangahua Depression are proposed. The total distance covered by Nothofagus migration from refugia during the postglacial is likely to be up to 10-15 km in most areas and up to 30 km down-stream along the flood plain of the lower Grey River. In some places postglacial migration covering only several kilometres is evident.

Westwards migration from Canterbury into north Westland across low passes in the Southern Alps also appears to have occurred in the postglacial period. Postglacial migration in the montane valleys of the Southern Alps may have been several times faster than in the study area.

12. The present limits of Nothofagus distribution in north Westland represent the cumulative effect of slow expansion from glacial refugia whose positions were determined by the relative intensity and duration of a sequence of adverse glacial and favourable inter-glacial periods.

13. Rimu and miro have predominantly continuous regeneration; southern rata, hard beech, Quintinia, red beech and kamahi have predominantly gap-phase regeneration. The species with gap-phase regeneration, with the exception of rata, are able to regenerate prolifically in large canopy gaps and following large-scale stand disturbance. The recruitment of rimu and miro to the canopy involves a long period of suppressed growth beneath the canopy of hardwood species. This period is from 100 to 500 years for rimu.

14. Rimu and miro have high shade tolerances, red beech and Quintinia are light-demanding and hard beech, southern rata and kamahi have intermediate tolerances.

15. Each canopy tree species is able to colonize bare surfaces as well as maintaining codominance in climax forest communities.

16. Hard beech, red beech, Quintinia and kamahi seedlings have high to very high densities, wide microsite preferences and fast to medium height growth rates. Rimu, miro and rata seedlings have low densities and low to very low rates of early establishment. Rimu and particularly rata small seedlings have restricted microsite requirements.

17. Large annual fluctuations in the rates of early establishment occurred in hard beech, red beech and rimu seedling populations in the period from 1974 to 1977.

18. Mortality rates of small seedlings ranged from 4.0% p.a. in rata to 23.3% p.a. in red beech. Large seedling mortality ranged from 1.3% p.a. in rata to 5.0% p.a. in hard beech. Most large seedling deaths appeared to follow a prolonged period of growth suppression. Animal browsing was not a significant cause of seedling deaths. Mortality rates of small seedlings, but not large seedlings, varied significantly from year to year.

19. A large proportion of seedlings of all species are capable of surviving for a number of years with low or negative height growth rates. Mean height growth rates in tagged large seedling populations ranged from 0.81 cm/yr in rimu to 3.65 cm/yr in red beech. Individual seedlings show much greater annual height increments.

20. Hard beech, Quintinia and kamahi have stable population structures, and rimu, miro, southern rata and red beech unstable population structures deficient in saplings,

poles and small canopy trees which are considered to represent past fluctuations in the rates of seedling establishment (rather than periodic, selective mortality among subcanopy individuals or differential diameter growth throughout the life span).

21. In rimu populations the rate of regeneration appears to have been constant and relatively high during the period from 1200 to 500 years ago with a subsequent steady decline through to the period 200-100 years ago. In the last 100 years an upsurge in regeneration, but not a return to the level pertaining before 500 years ago, is apparent. In miro populations there is evidence for a regeneration decline which paralled in timing and extent the decline in rimu. A regeneration decline began in southern rata in the period from 200 to 400 years ago and in red beech in the period from 150 to 200 years ago. A recent upsurge in regeneration has not occurred in most southern rata populations.

22. It is postulated that the long-term changes in regeneration rates in rimu, southern rata, miro and red beech populations resulted from catastrophic damage to the hardwood component of the forest canopy within the period 300-500 years ago. This damage led to an immediate upsurge of southern rata and possibly red beech regeneration and to a continuing suppression of rimu and miro regeneration by the vigourously regenerating hardwood species.

23. A definite causal relationship between past changes in regeneration rates and the known biotic and climatic changes of the past 500 years cannot be established. The introduction of seed-eating rats

and the extinction of understorey browsing animals during the Polynesian era, increased incidence of drought, decreased insolation and greater storminess could be the causal factors involved.

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REFERENCES

ADAMS, J.A.; MEW, G. 1976: Interim report on the limitations for exotic forestry of the soils of the Grey Valley, South Island. New Zealand Soil Bureau Record 47. N.Z. Soil Bureau, D.S.I.R., Wellington.

ALLAN, H.H. 1926: Vegetation of Mount Peel, Canterbury, New Zealand. Part 1. The Forest and Shrublands. Proceedings of the N.Z. Institute 56 : 37 - 51.

_____ 1961: Flora of New Zealand. Vol. 1. Government Printer, Wellington. 1085 pp.

ALDER, G.M.; HARPER, K.T. 1969: Age profiles in aspen forests of Utah and Northern Arizona. Utah Academy Proceedings 46 : 166.

ARMSTRONG, J.M.; BUSSELL, W.T. 1964: An ecological study of the red beech forest at Cascade Creek, Fiordland. Science Record 14 : 56.

ARNOLD, B.C. 1960: Mycorrhizal infection of germinating seedlings of Nothofagus cliffortioides. Pacific Science 14: 248-50.

AUCLAIR, A.N.; COTTAM, G. 1971: Dynamics of black cherry (Prunus serotina Erhr.) in southern Wisconsin oak forests. Ecological Monographs 41 : 153-77.

BARTON, I.L. 1972: On the vegetation of the Hunua Ranges, Auckland. N.Z. Journal of Botany 10: 8-26.

BAYLIS, G.T.S.; 1960: The significance of mycorrhizas and root nodules in the New Zealand vegetation. Transactions of the Royal Society of N.Z. 89 : 45-50

_____ 1971: Endogonaceous mycorrhizas synthesised in Leptospermum (Myrtaceae). N.Z. Journal of Botany 9 : 293-6.

BAYLIS, G.T.S. 1980: Mycorrhizas and the spread of beech. N.Z. Journal of Ecology 3 : 151-3.

BEARD, J.S. 1946: The Mora forests of Trinidad, British West Indies. Journal of Ecology 33 : 173-92.

BEVERIDGE, A.E. 1964: Dispersal and destruction of seed in central North Island podocarp forests. Proceedings of the N.Z. Ecological Society 11 : 48-55.

_____ 1973: Regeneration of podocarps in a central North Island forest. N.Z. Journal of Forestry 18 : 23-25

_____ 1977: Notes on the silviculture of kauri. In: Chavasse, C.G.R. (ed.), N.Z. Institute of Foresters. Forestry Handbook, pp. 125-30.

_____; DANIEL, M.J. 1965: Observations on a high population of brown rats (Rattus norvegicus Berkenhout 1767) on Mokoia Island, Lake Rotorua. N.Z. Journal of Science 8: 174-91.

_____; FRANKLIN, D.A. 1977: Notes on the silviculture of rimu. In: Chavasse, C.G.R. (ed.), N.Z. Institute of Foresters. Forestry Handbook, pp. 121-25.

BIBBY, K.M. 1953: Laboratory germination tests of Nothofagus seed. Forest Research Notes 1 No.7. Forest Research Institute, N.Z. Forest Service.

BORMANN, F.H.; LIKENS, G.E. 1979: Pattern and process in a forested ecosystem. Springer-Verlag, New York. 253 pp.

BOWEN, F.E. 1964: Sheet 15 Buller (1st Ed.) "Geological Map of New Zealand 1 : 250 000". Department of Scientific and Industrial Research, Wellington.

BRAY, J.R. 1956: Gap phase replacement in a maple-basswood forest. Ecology 37 598-600.

BROWN, G.D.; STICHBURY, B.B. 1973: A survey of regeneration after strip felling in terrace rimu forest, South Westland. N.Z. Forest Service, Forest Research Institute, Indigenous Silviculture Report, No.12 (unpubl.).

BUDOWSKI, G. 1970: The distinction between old secondary and climax species in tropical Central American lowland forests. Tropical Ecology 11 : 44-48.

BUNN, E.H. 1965: Rangataua Forest Compt. 215.1963 mast year seedfall study (Appendix). In: Franklin, D.A. (Comp.), Beech Forestry in New Zealand. N.Z. Forest Service Forest Research Institute (unpubl.), pp. 149-52.

BURNS, M.M. 1931: Chemical aspects of the soil of the rimu forests. Te Kura Ngahere 3 : 5-16.

BURROWS, C.J. 1965: Some discontious distributions of plants within New Zealand and their ecological significance - Part II: Disjunctions between Otago-Southland and Nelson-Marlborough and related distribution patterns. Tuatara 13 : 9-29.

_____ 1973: The ecological niches of Leptospermum scoparium and L. ericoides (Angiospermae : Myrtaceae) Mauri Ora 1 : 5-12

_____ 1977: Forest vegetation. In: Burrows, C.J. (ed.), Cass. History and Science in the Cass District, Canterbury, New Zealand. University of Canterbury, pp. 233-57.

_____ 1978: The Quaternary ice ages in New Zealand: a framework for biologists. Mauri Ora 6: 69-96.

_____ 1979: A chronology for cool-climate episodes in the Southern Hemisphere 12 000 - 1 000 year B.P. Palaeogeography, Palaeoclimatology, Palaeoecology 27 : 287-347.

_____; DOBSON, A.T. and THIRD YEAR PLANT ECOLOGY CLASS. 1975: Population structure in a beech-podocarp forest near Bell Hill, Westland. Mauri Ora 3 : 125-33.

BURROWS, C.J.; GREENLAND, D.E. 1979: An analysis of the evidence for climatic change in New Zealand in the last thousand years: evidence from diverse natural phenomena and from instrumental records. Journal of the Royal Society of N.Z. 9 : 321-73.

_____ 1982: On New Zealand climate within the last 1000 years. N.Z. Journal of Archeology (in press).

CAMERON, R.J. 1954: Mosaic or cyclic regeneration in North Island podocarp forests. N.Z. Journal of Forestry 7 : 55-65.

_____ 1960: Natural regeneration of podocarps in the forests of the Whirinaki River Valley. N.Z. Journal of Forestry 8 : 337-54.

_____ 1963: A study of the rooting habits of rimu and tawa in pumic soils. N.Z. Journal of Forestry 8 : 771-85.

CALDER, J.W.; WARDLE, P. 1969: Succession in subalpine vegetation at Arthur's Pass, New Zealand. Proceedings of the N.Z. Ecological Society 16 : 36-47.

CAMPBELL, D.J. 1978: The effects of rats on vegetation. In; The Ecology and Control of Rodents in New Zealand Nature Reserves. Department of Lands and Survey Information Series No. 4, pp. 99-120.

CLARKE, C.M.H. 1976: Eruption, deterioration and decline of the Nelson red deer herd. N.Z. Journal of Forestry Science 5 : 235-49.

CLAYTON-GREENE, K.A. 1977: Structure and origin of Libocedrus bidwillii stands in the Waikato district, New Zealand. N.Z. Journal of Botany 15 : 19-28.

CLIMO, F.M. 1975: The land snail fauna. In: Kuschel, G. (Ed.) Biogeography and Ecology in New Zealand. W. Junk, The Hague.

COCKAYNE, L. 1926: Monograph on New Zealand Beech Forests. Part I. The ecology of the forests and taxonomy of the beeches. N.Z. State Forest Service Bulletin No.4. Government Printer, Wellington.

COCKAYNE, L. 1928: The Vegetation of New Zealand. 2nd ed. W. Engelmann, Leipzig. 456 pp.

_____; ATKINSON, E. 1926: On the New Zealand wild hybrids of Nothofagus. Genetica 8 : 1-42

CONWAY, M.J. 1949: Beetle damage to beech forest. N.Z. Journal of Forestry 6 : 67-8

_____ 1952: The silviculture of red beech in Nelson and Westland. N.Z. Journal of Forestry 6 : 291-308.

COULTER, J.D. 1973: Ecological aspects of the climate. In: Williams, G.R. (ed.), The Natural History of New Zealand Reed, Wellington, pp. 28-60.

CRANWELL, L.M. 1963: Nothofagus : living and fossil. In: Pacific Basin Biogeography. Gressitt, J.L. (Ed.) 10th Pacific Science Congress, 1961. Bishop Museum Press, Honolulu. Pp 387-400.

CUMBERLAND, K.B. 1962: Climatic change or cultural interference? In: Land and Livelihood, Geographical Essays in Honour of George Jobberns. (Ed. M. McCaskill). N.Z. Geographical Society, Christchurch. Pp 88-142.

DANSEREAU, P. 1964: Six problems in New Zealand vegetation. Bulletin of the Torrey Botanical Club 91 : 114-40.

DARLINGTON, P.J. 1965: Biogeography of the Southern End of the World. Harvard University Press. 236 pp.

DAVIS, M.B. 1976: Pleistocene biogeography of temperate deciduous forests. Geoscience and Man 13 : 13-26.

DICKSON, M. 1972: Palynology of a late Oturi Interglacial and early Otira Glacial sequence from Sunday Creek (S 51), Westland, New Zealand. N.Z. Journal of Geology and Geophysics 15 : 590-8.

DODSON, J.R. 1978: A vegetation history from north-east Nelson, New Zealand. N.Z. Journal of Botany 16 : 371-8.

DRUCE, A.P.; ATKINSON, I.A.E. 1958: Forest variation in the Hutt Catchment. Proceedings of the N.Z. Ecological Society 6 : 41-5.

ELDER, N.L. 1941: Nothofagus regeneration in the Kaweka Range. N.Z. Journal of Forestry 4 : 324-7.

_____ 1962: Vegetation of the Kaimanawa Ranges. Transactions of the Royal Society of N.Z. (Botany) 2 : 1-37

_____ 1963: Evidence of climatic change from the vegetation of the North Island. Proceedings of the N.Z. Ecological Society 10 : 45-8.

_____ 1965: Vegetation of the Ruahine Range: an introduction. Transactions of the Royal Society of N.Z. (Botany) 3 : 13-66.

ESLER, A.E. 1967: The vegetation of Kapiti Island. N.Z. Journal of Botany 5 : 353-93.

EVANS, G.C. 1956: An area survey method of investigating the distribution of light intensity in woodlands, with particular reference to sunflecks. Journal of Ecology 44 : 391-428.

FLEMING, C.A. 1977: The history of life in New Zealand forests. N.Z. Journal of Forestry 22 : 249-62.

FORCIER, L.K. 1975: Reproductive strategies and the co-occurrence of climax tree species. Science 189 : 808-810.

FORSTER, R.R. 1954: The New Zealand Harvestmen (suborder Laniatores). Canterbury Museum Bulletin 2 329 pp.

FRANKLIN, D.A. 1965a: Growth rates of beech. In: Franklin, D.A. (Comp.), Beech Forestry in New Zealand. N.Z. Forest Service Forest Research Institute (unpubl.) pp. 62-69.

_____ 1965b: Site requirements and tolerances of New Zealand beech species. In: Franklin, D.A. (Comp.), Beech Forestry in New Zealand. N.Z. Forest Service, Forest Research Institute (unpubl.) pp. 58-61.

FRANKLIN, D.A. 1967: The synecology of the Tararua indigenous forests. N.Z. Forest Service, Forest Research Institute Technical Paper 53 : 39 pp.

_____ 1968: Biological flora of New Zealand. 3. Dacrydium cupressinum Lamb. (Podocarpaceae) Rimu. N.Z. Journal of Botany 6 : 493-513.

_____ 1969a: Growth rings in rimu from South Westland terrace forest. N.Z. Journal of Botany 7 : 177-88.

_____ 1969b: Trials to improve regeneration in terrace rimu forest, Westland. N.Z. Forest Service, Forest Research Institute, Indigenous Silviculture Report No.2 (unpubl.)

_____ 1977: Beech seedfalls in some South Island lowland forests. Beech Research News, Scientific Co-ordinating Committee for Beech Research No.5 : 9-13.

_____; NICHOLLS, J.L. 1974: Grey forest class map. 1:250,000. N.Z. Forest Service Mapping Series 6 Sheet No.18.

FRASER, L.; VICKERY, J.W. 1938: The Ecology of the Upper Williams River and Barrington tops districts. II The rain-forest formations. Proceedings of the Linnaen Society of New South Wales 63 : 139-84.

FRITZ, E. 1929: Some popular fallacies concerning redwood. Madrono 1 : 221-24.

GAGE, M. 1965: Some characteristics of Pleistocene cold climates in New Zealand. Transactions of the Royal Society of N.Z. (Geology) 3 : 11-21.

_____ 1977: Glacial geology. In: Burrows, C.J. (ed.), Cass. History and Science in the Cass District, Canterbury, New Zealand. University of Canterbury. pp. 67-77.

GARNIER, B.J. 1958: The Climate of New Zealand: a Geographic Survey. Arnold, London. 191 pp.

GIBB, J.A.; FLUX, J.E.C. 1973: Mammals. In: Williams, G.R. (ed.) The Natural History of New Zealand. Reed, Wellington, pp. 334-71.

GIBBS, H.S.; MERCER, A.D.; COLLIE, T.W. 1950: Soils and agriculture of Westland, New Zealand. N.Z. Soil Bureau Bulletin 2. N.Z. Soil Bureau, D.S.I.R., Wellington, 24 pp.

GRANT, P.J. 1963: Forests and recent climatic history of the Huiarau Range, Hawke's Bay. Transactions of the Royal Society of N.Z. (Botany) 2 : 143-72.

_____ 1965: Major regime changes of the Tukituki River, Hawke's Bay, since about 1650 A.D. Journal of Hydrology (N.Z.) 4 : 17-30.

GREGG, D.R. 1964: Sheet 18. Hurunui (1st Ed.) "Geological Map of New Zealand 1 : 250 000". Department of Scientific and Industrial Research, Wellington.

GREENWOOD, R.M.; ATKINSON, I.A.E. 1977: Evolution of divaricating plants in New Zealand in relation to moa browsing. Proceedings of the N.Z. Ecological Society 24 : 21-33.

GRIGGS, R.F. 1946: The timberlines of northern America and their interpretation. Ecology 27 : 275-89.

GRIME, J.P. 1979: Plant Strategies and Vegetation Processes. John Wiley and Sons, Chichester. 222 pp.

_____; JEFFREY, D.W. 1965: Seedling establishment in vertical gradients of sunlight. Journal of Ecology 53 : 621-42

GRINSTED, M.J.; WILSON, A.T. 1979: Variations of $^{13}C/^{12}C$ ratio in cellulose of Agathis australis (kauri) and climatic change in New Zealand during the last millenium. N.Z. Journal of Science 22 : 55-61.

GRUBB, P.J. 1977: The maintence of species-richness in plant communities : the importance of the regeneration niche. Biological Reviews 52 : 107-45.

HARCOMBE, P.A.; MARKS, P.L. 1978: Tree diameter distributions and replacement processes in Southeast Texas forests. Forest Science 24 : 153-66.

HARLEY, J.L. 1969: The Biology of Mycorrhiza. Leonard Hill, London. 2nd Ed. 334 pp.

HARPER, J.L. 1977: Population Biology of Plants. Academic Press, London. 892 pp.

HARTSHORN, G.S. 1978: Tree falls and tropical forest dynamics. In: Tomlinson, P.B.; Zimmermann, M.H. (Eds.) Tropical trees as living systems. Cambridge University Press.

HERBERT, J. 1978: Forest pattern and regeneration ecology of the Rangitoto-Hauhungaroa forests. N.Z. Forest Service seminar, Taupo: Management Proposals for State Forests of the Rangitoto and Hauhungaroa Ranges, Central North Island. N.Z. Forest Service, Wellington. 26 pp.

_____ 1980: Structure and growth of dense podocarp forest at Tihoi, Central North Island, and the impact of selective logging. N.Z. Journal of Forestry 25 : 44-57.

HETT, J.M. 1971: A dynamic analysis of age in sugar maple seedlings. Ecology 52 : 1071-74.

_____; LOUCKS, O.L. 1976: Age structure models of balsan fir and eastern hemlock. Journal of Ecology 64 : 1029-44.

HOCKING, G.H.; KENDERDINE, C.A.B. 1945: Silvicultural observations on a central North Island beech forest. N.Z. Journal of Forestry 5 : 90-102.

HOEG, H.I. 1978: The immigration of Picea abies to southeastern Norway with special regard to Telemark (a preliminary report). Norwegian Journal of Botany 25 : 19-21.

HOLLOWAY, J.T. 1946: Forest associations of the Longwood Range, Southland. N.Z. Journal of Forestry 5 : 199-209.

HOLLOWAY, J.T. 1950: Deer and the forests of Western Southland. N.Z. Journal of Forestry 6 : 123-37.

_____ 1954: Forests and climates in the South Island of New Zealand. Transactions of the Royal Society of N.Z. 82 : 329-410.

HORN, H.S. 1974: The ecology of secondary succession. Annual Review of Ecology and Systematics 5 : 25-37.

HOWARD, T.M.; ASHTON, D.H. 1973: The distribution of Nothofagus cunninghamii rainforest. Proceedings of the Royal Society of Victoria 86 : 47-76.

HUGHES, H.R. 1975: Regeneration of semi-pakihi forest, Granville State Forest, Westland. Beech Research News, Scientific Co-ordinating Committee No.3 : 9-15.

HUTCHINSON, F.E. 1928: A hypothesis in regard to the Westland rimu bush. Te Kura Ngahere 2 (3) : 3-12.

_____ 1932: The life history of the Westland rimu stands. Te Kura Ngahere 3 : 54-61.

JANSEN, H.S.; WARDLE, P. 1971: Comparison between ring age and ^{14}C age in rimu trees from Westland and Auckland. N.Z. Journal of Botany 9 : 215-6.

JONES, E.W. 1945: The structure and reproduction of the virgin forest of the north temperate zone. New Phytologist 44 : 130-48.

JOHNSTON, A.D. 1972: Management of West Coast beech forests. N.Z. Journal of Forestry 17 : 180-88.

JUNE, S.R. 1974: The germination, growth and survival of red beech (Nothofagus fusca) seedlings in relation to forest regeneration. M.Sc. thesis, Massey University. 124 pp.

_____ 1977: A major range extension for hard beech (Nothofagus truncata) in the South Island (Note) Mauri Ora 5 : 119-121.

JUNE, S.R.; OGDEN, J. 1975: Studies on the vegetation of Mount Colenso, New Zealand. 3. The population dynamics of red beech seedlings. Proceedings of the N.Z. Ecological Society 22 : 61-6.

_____ 1978: Studies on the vegetation of Mount Colenso, New Zealand. 4. An assessment of the processes of canopy maintenance and regeneration strategy in a red beech (Nothofagus fusca) forest. N.Z. Journal of Ecology 1 : 7-15.

KATZ, A. 1980: Structure and growth of dense podocarp forest in Whirinaki. Indigenous Forest Management Report No.25, Forest Research Institute, N.Z. Forest Service (unpublished).

KEETON, W.T. 1980: Biological Science. 3rd Ed. Norton and Co.. New York. 526 pp.

KEEVER, C. 1973: Distribution of major forest trees in southeastern Pennsylvania. Ecological Monographs 43 : 303-27.

KERSHAW, D.J. 1980: Defoliation and mortality of Nothofagus fusca (red beech) at Maruia, Nelson. Forest Entomology Report No.47, N.Z. Forest Service, Wellington. 7 pp.

KIRKLAND, A. 1961: Preliminary notes on seeding and seedlings in red and hard beech forests of North Westland and the silvicultural implications. N.Z. Journal of Forestry 8 : 482-97.

_____ 1973: Beech Forests. N.Z. Forest Service, Wellington. 48 pp.

_____; TROTMAN, I.G. 1974: Indigenous forests of New Zealand, 1974. Part 2. Appendices - containing forest descriptions and statistics. Contribution paper to the Forestry Development Conference, Wellington, 19-21 November 1974. N.Z. Forest Service, Wellington. 119 pp.

LEAK, W.B. 1975: Age distribution in virgin red spruce and northern hardwoods. Ecology 56 : 1451-4.

LEAK, W.B.; GRABER, R.F. 1974: A method for detecting migration of forest vegetation. Ecology 55 : 1425-27.

LEE, K.E. 1959: The Earthworm Fauna of New Zealand. N.Z. Department of Scientific and Industrial Research Bulletin 130. 486 pp.

LINTOTT, W.H.; BURROWS, C.J. 1973: A pollen diagram and macrofossils from Kettlehole Bog, Cass, South Island, New Zealand. N.Z. Journal of Botany 11 : 269-82.

LORIMER, C.G. 1980: Age structive and disturbance history of a Southern Appalachian virgin forest. Ecology 61 : 1169-84.

MABIN, M.C.G. 1976: The glacial sequence in the Middle Maruia Valley, South-east Nelson, New Zealand. M.Sc. thesis, University of Canterbury, Christchurch.

MARK, A.F.; SCOTT, G.A.M.; SANDERSON, F.R.; JAMES, P.W. 1964: Forest succession on landslides above Lake Thomson, Fiordland. N.Z. Journal of Botany 2 : 60-89.

MARKS, P.L. 1974: The role of pin cherry (Prunus pensylvanica L.) in the maintenance of stability in northern hardwood ecosystems. Ecological Monographs 44 : 73-88.

MASTERS, S.E.; HOLLOWAY, J.T.; McKELVEY, P.J. 1957: The National Forest Survey of New Zealand; Vol. I, The Indigenous Forest Resources of New Zealand. Government Printer, Wellington.

MATHEWS, W.H. 1967: Profiles of late Pleistocene glaciers in New Zealand. N.Z. Journal of Geology and Geophysics 10 : 146-63.

McGLONE, M.S. 1980: Late Quaternary vegetation history of Central North Island, New Zealand. Ph.D. thesis, University of Canterbury. 250 pp.

_____; MOAR, N.T. 1977: The Ascarina decline and post-glacial climatic change in New Zealand. N.Z. Journal of Botany 15 : 485-9.

McGLONE, M.S.; TOPPING, W.W. 1977: Aranuian (post-glacial) pollen diagrams from the Tongariro region, North Island, New Zealand. N.Z. Journal of Botany 15 : 749-60.

McKELLAR, I.C. 1960: Pleistocene deposits of the Upper Clutha Valley, Otago, New Zealand. N.Z. Journal of Geology and Geophysics 3 : 432-60.

McKELLAR, M.H. 1973: Dispersal of Nothofagus pollen in eastern Otago, South Island, New Zealand. N.Z. Journal of Botany 11 : 305-10.

McKELVEY, P.J. 1953: Forest colonization after recent volcanicity at West Taupo. N.Z. Journal of Forestry 6 : 435-48.

_____ 1955: A note on the forest edge at Te Whaiti. N.Z. Journal of Forestry 7 : 77-80

_____ 1959: Animal damage in North Island protection forests. N.Z. Science Review 17 : 28-34

_____ 1963: The synecology of the West Taupo indigenous forest. N.Z. Forest Service Bulletin 14 : 127 pp.

_____ 1973: The pattern of the Urewera forests. N.Z. Forest Service Research Institute Technical Paper No.59 : 48 pp.

_____; NICHOLLS, J.L. 1957: A provisional classification of North Island forests. N.Z. Journal of Forestry 7 : 84-101.

McQUEEN, D.R. 1951: Succession after forest fires in the Southern Tararua Mountains. Bulletin of the Wellington Botanical Society No.24 : 10-19

MEJSTRIK, V. 1972: The classification and relative frequency of mycorrhizae in Nothofagus solandri var. cliffortioides. N.Z. Journal of Botany 10 : 243-53.

MEYER, H.A. 1952: Structure, growth and drain in balanced uneven-aged forests. Journal of Forestry 50 : 85-92.

MEW, G. 1980: Soils of Greymouth-Hokitika region, South Island, New Zealand. N.Z. Soil Survey report 58. N.Z. Soil Bureau, Department of Scientific and Industrial Research, Wellington.

_____; WEBB, T.H.; ROSS, C.W.; ADAMS, J.A. 1975: Soils of the Inangahua Depression, South Island, New Zealand. N.Z. Soil Survey Report 17. N.Z. Soil Bureau, D.S.I.R., Wellington.

_____; LEAMY, M.L. 1977: Some pedological trends from recent West Coast soil surveys and their relevance to forest use. N.Z. Journal of Forestry Science 7 : 151-61.

MILLER, P.C. 1970: Age distributions of Spruce and Fir in beetle-killed forests on the White River Plateau, Colarado. American Midland Naturalist 83 : 206-212.

MILLIGAN, R.H. 1972: A review of beech forest pathology. N.Z. Journal of Forestry 17 : 201-11.

MOAR, N.T. 1970: Recent pollen spectra from three localities in the South Island, New Zealand. N.Z. Journal of Botany 8 : 210-21.

_____ 1971: Contributions to the Quaternary history of the New Zealand flora. 6. Aranuian pollen diagrams from Canterbury, Nelson and North Westland, South Island. N.Z. Journal of Botany 9 : 80-145.

_____ 1973: Late Pleistocene vegetation and environment in Southern New Zealand. In: Van Zinderen Bakker (ed.), Palaeoecology of Africa, the Surrounding Islands and Antarctica, Vol. 8. Balkema, Cape Town, pp. 179-198

_____ 1980: Late Otiran and early Aranuian grassland in central South Island. N.Z. Journal of Ecology 3 : 4-12.

_____; LINTOTT, W.H. 1977: Post-glacial history of vegetation at Cass. In: Burrows, C.J. (ed.), Cass. History and Science in the Cass District, Canterbury, New Zealand. University of Canterbury, pp. 147-56.

MOAR, N.T.; SUGGATE, R.P. 1973: Pollen analysis of late Otiran and Aranuian sediments at Blue Spur Road (s 51), north Westland. N.Z. Journal of Geology and Geophysics 16 : 321-31.

_____ 1979: Contributions to the Quaternary history of the New Zealand flora. 8. Interglacial and glacial vegetation in the Westport District, South Island. N.Z. Journal of Botany 17 : 361-87.

MOLLOY, B.P.J. 1969: Evidence for post-glacial climatic changes in New Zealand. Journal of Hydrology (New Zealand 8 : 56-67.

_____; BURROWS, C.J.; COX, J.E.; JOHNSTON, J.A.; WARDLE, P. 1963: Distribution of subfossil forest remains, eastern South Island, New Zealand. N.Z. Journal of Botany 1 : 68-77.

_____; COX, J.E. 1972: Subfossil forest remains and their bearing on forest hisotry in the Rakaia catchment, Canterbury, New Zealand. N.Z. Journal of Botany 10 : 267-76.

MORRIS, J.Y. 1959: Beech forest types and management potential in North Westland. N.Z. Journal of Forestry 8 : 91-100.

MORRISON, T.M. 1956: Mycorrhizae of silver beech. N.Z. Journal of Forestry 7 : 47-60.

NAMKOONG, G.; ROBERDS, J.H. 1974: Extinction probabilities and the changing age structure of redwood forests. The American Naturalist 108 : 355-68.

NATHAN, S.; MOAR, N.T. 1973: Age and correlation of late Quaternary terraces in the lower Inangahua Valley, West Coast, South Island, New Zealand. Journal of the Royal Society of New Zealand 3 : 409-14.

NG, F.S.P. 1978: Stategies of establishment in Malayan forest trees. In: Tomlinson, P.B.; Zimmermann M.H. (Eds.) Tropical trees as living systems. Cambridge University Press. pp. 129-62.

NICHOLLS, J.L. 1956: The historical ecology of the indigenous forest of the Taranaki Upland. N.Z. Journal of Forestry 7 : 17-34.

N.Z. GEOLOGICAL SURVEY. 1973: Quaternary Geology - South Island, 1 : 1 000 000 (1st Ed.) N.Z. Geological Survey Miscellaneous Series Map 6. D.S.I.R., Wellington.

N.Z. FOREST SERVICE. 1974: New Zealand Indigenous Forests (1st Ed.) 1 : 1 000 000. N.Z. Forest Service Mapping Series 15.

N.Z. METEOROLOGICAL SERVICE. 1977: Temperature frequencies for selected New Zealand Stations. N.Z. Meteorological Service Miscellaneous Publication 158.

NEW ZEALAND SOIL BUREAU. 1968: General survey of the soils of the South Island, New Zealand. N.Z. Soil Bureau Bulletin 27. N.Z. Soil Bureau, D.S.I.R., Wellington, 404 pp.

NEW ZEALAND SOIL BUREAU 1969: Soil map of the South Island, New Zealand. Sheet 3 1 : 250 000. N.Z. Soil Bureau, D.S.I.R., Wellington.

NORTON, D.A. 1981: Dendroclimatology and population dynamics of Libocedrus bidwillii Hook. f., Westland, New Zealand. Report No. WS 519. Ministry of Works and Development. Christchurch, N.Z. 78 pp.

ODUM, E.P. 1971: Fundamentals of Ecology. 3rd Ed. Saunders, Philadelphia. 574 pp.

OGDEN, J. 1971: Studies on the vegetation of Mount Colenso. 2. The population dynamics of red beech. Proceedings of the N.Z. Ecological Society 18 : 66-75.

_____ 1978: On the diameter growth rates of red beech (Nothofagus fusca) in different parts of New Zealand. N.Z. Journal of Ecology 1 : 16-18.

OLIVER, C.D.; STEPHENS, E.P. 1977: Reconstruction of a mixed species forest in Central New England. Ecology 58 : 562-572.

O'LOUGHLIN, C.L.; GAGE, M. 1975: A report on the status of slope erosion on selected steep areas, West Coast Beech Project Area. N.Z. Forest Service, Forest Research Institute Report (unpublished). 37 pp.

PHILIPSON, W.R. 1965: The New Zealand genera of Araliaceae. N.Z. Journal of Botany 3 : 333-341

POCKNALL, D.T. 1980: Modern pollen rain and Aranuian vegetation from Lady Lake, north Westland, New Zealand. N.Z. Journal of Botany 18 : 275-84.

POOLE, A.L. 1937: A brief ecological survey of the Pukekura State Forest, South Westland. N.Z. Journal of Forestry 4 : 78-85

_____ 1948: The flowering of beech. N.Z. Journal of Forestry 5 : 422-7.

_____ 1951: Hybrid Southern beeches. N.Z. Journal of Forestry 6 : 250-3

POORE, M.E.D. 1968: Studies in Malaysian Rain Forest. I. The forest on Triassic Sediments in Jengka Forest Reserve. Journal of Ecology 56 : 143-96.

PORTER, S.C. 1975: Equilibrium-line altitudes of late Quaternary glaciers in the Southern Alps, New Zealand. Quaternary Research 5 : 27-47.

PREEST, D.S. 1963: A note on the dispersal characteristics of the seed of the New Zealand podocarps and beeches, and their biogeographical significance. In: Gressitt, J.L. (Ed.), Pacific Basin Biography. 10th Pacific Science Congress 1961, Bishop Museum Press, Honolulu, pp. 415-24.

PULLAR, W.A. 1970: Periods of recent infilling of the Gisborne Plains basin : associated marker beds and changes in the shoreline. N.Z. Journal of Science 13 : 410-34.

RAESIDE, J.D. 1948: Some post-glacial climatic changes in Canterbury and their effect on soil formation. Transactions and Proceedings of the Royal Society of N.Z. 77 : 153-71.

RAWLINGS, G.B. 1953: Insect epidemics on forest trees in New Zealand. N.Z. Journal of Forestry 6 : 405-12.

REID, J.S. 1948: Regeneration in indigenous montane forest after fire. N.Z. Journal of Forestry 5 : 436.

RICHARDS, P.W. 1952: The tropical rain forest. Cambridge, England. 450 pp.

RICKLEFS, R.E. 1973: Ecology Nelson, London. 861 pp.

RIDLEY, H.N. 1930: The Dispersal of Plants throughout the World. Reeve and Co. Kent 744 pp.

RINEY, T.; WATSON, J.S.; BASSETT, C.; TURBOTT, E.G.; HOWARD, W.E. 1952: Lake Monk Expedition, an ecological study in southern Fiordland. N.Z. Department of Scientific and Industrial Research Bulletin 135, 75 pp.

ROBBINS, R.G. 1962: The podocarp-broadleaf forests of New Zealand. Transactions of the Royal Society of New Zealand (Botany) 1 : 33-75

RUSSELL, J.B. 1980: Pollen diagrams from montane Canterbury, New Zealand. Ph.D. thesis, University of Canterbury, Christchurch. 248 pp.

SARUKHAN, J. 1980: Demographic problems in tropical systems. In: Solbrig, O.T. (Ed.) Demography and evolution in plant populations. Botanical Monographs 15, Blackwell, Oxford. pp. 161-86.

SILVESTER, W.B. 1964: Forest regeneration problems in the Hunua Range, Auckland. Proceedings of the N.Z. Ecological Society 11 : 1-5.

SINGER, R. 1969: Forest mycology and forest communities in South America. II Mycorrhiza sociology and fungus succession in the Nothofagus dombeyi - Austrocedrus chilensis woods of Patagonia. In: North American Conference of Mycorrhizae, University of Illinois. United States Department of Agriculture.

SIX DIJKSTRA, H.G. 1981: Architecture and age structure of terrace rimu forest at Saltwater, South Westland, New Zealand and the effect of selective logging by the parallel hauling method. M. Forestry Sc. thesis, University of Canterbury 155 pp.

SOKAL, R.R.; ROHLF, F.J. 1969: Biometry. The Principles and Practice of Statistics in Biological Research. W.H. Freeman and Company, San Francisco, 776 pp.

STEWART, G.H.; VEBLEN, T.T. 1981: The dynamics of kaikawaka stands. What's New in Forest Research, Forest Research Institute, Rotorua. No.95. 4 pp.

SUGGATE, R.P. 1950: Franz Josef and other glaciers of the Southern Alps, New Zealand. Journal of Glaciology 1 : 422-9

_____ 1965: Late Pleistocene geology of the northern part of the South Island, New Zealand. N.Z. Department of Scientific and Industrial Research Geological Survey Bulletin n.s. 77, 91 pp.

_____; MOAR, N.T. 1970: Revision of the chronology of the late Otira Glacial. N.Z. Journal of Geology and Geophysics 13 : 742-6.

TAPPEINER, J.C.; HELMS, J.A. 1971: Natural regeneration of Douglas Fir and White Fir on exposed sites in the Sierra Nevada of California. The American Naturalist 86 : 358-69.

TRAVERS, W.W.G. 1961: Rimu seeding in the terrace podocarp forests of South Westland. N.Z. Journal of Forestry 8 : 508-11.

TRENBERTH, K.E. 1977: Climate and climate change, a New Zealand perspective. N.Z. Meteorological Service Miscellane ous Publication 161. 51 pp.

VAARTAJA, O. 1952: Forest Lumus quality and light conditions as factors influencing damping-off. Phytopathology 42: 501-6

VEBLEN, T.T.; SCHLEGEL, F.M.; ESCOBAR, B. 1980: Structure and dynamics of old-growth Nothofagus forests in the Valdivian Andes, Chile. Journal of Ecology 68 : 1-31.

_____; STEWART, G.H. 1980: Comparison of forest structure and regeneration on Bench and Stewart Islands, New Zealand. N.Z. Journal of Ecology 3 : 50-68.

WALKER, D. 1966: Vegetation of the Lake Ipea Region, New Guinea Highlands. 1. Forest, Grassland and Garden. Journal of Ecology 54 : 503:33.

WARREN, G. 1967: Sheet 17 Hokitika (1st Ed.) Geological Map of New Zealand 1 : 250 000. Department of Scientific and Industrial Research, Wellington.

WARDLE, J.A. 1970a: The ecology of Nothofagus solandri. 1. The distribution and relationship with other major forest and scrub species. N.Z. Journal of Botany 8 : 494-531.

_____ 1970b: The ecology of Nothofagus solandri. 3. 3. Regeneration. N.Z. Journal of Botany 8: 571-608.

_____ 1974: Influence of introduced mammals on the forest and shrublands of the Grey River headwaters. N.Z. Journal of Forestry Science 4 : 459-86.

_____; HAYWARD, J. 1970: The forests and scrublands of the Taramakau and the effects of browsing by deer and chamois. Proceedings of the N.Z. Ecological Society 17 : 80-91.

WARDLE, P. 1962: Subalpine forest and scrub in the Tararua Range. Transactions of the Royal Society of N.Z. (Botany) 1 : 77-89.

WARDLE, P. 1963a: Evolution and distribution of the New Zealand flora, as affected by Quaternary climates. N.Z. Journal of Botany 1 : 3-17.

_____ 1963b: The regeneration gap of New Zealand gymnosperms. N.Z. Journal of Botany 1 : 301-15.

_____ 1963c: Vegetation studies on Secretary Island, Fiordland. Part 5. Population structure and growth of rimu (Dacrydium cupressinum). N.Z. Journal of Botany 1 : 208-14.

_____ 1964: Facets of the distribution of forest vegetation in New Zealand. N.Z. Journal of Botany 2 : 352-66.

_____ 1966: Biological flora of New Zealand. 1. Weinmannia racemosa Linn. F. (Cunoniaceae), Kamahi. N.Z. Journal of Botany 4 : 114-31.

_____ 1967: Biological flora of New Zealand. 2. Nothofagus menziesii (Hook. f.) Oerst. (Fagaceae) silver beech. N.Z. Journal of Botany 5 : 276-302

_____ 1970: Pleistocene snow lines in the Fox Glacier area (Letter to the Editor). N.Z. Journal of Geology and Geophysics 13 : 560.

_____ 1971a: An explanation for alpine timberline. N.Z. Journal of Botany 9 : 549-54

_____ 1971b: Biological flora of New Zealand. 6. Metrosideros umbellata Cav. (Syn. M. Lucida (Forst. f.) A. Rich) (Myrtaceae) Southern Rata. N.Z. Journal of Botany 9 : 645-71.

_____ 1973a: Native vegetation. In: Williams, G.R. (Ed.), The Natural History of New Zealand. Reed, Wellington, pp. 155-69.

_____ 1973b: Variations of the glaciers of Westland National Park and the Hooker Range, New Zealand. N.Z. Journal of Botany 11 : 349-88.

_____ 1974: The kahikatea (Dacrycarpus dacrydioides) forest of South Westland. Proceedings of the N.Z. Ecological Society 21 : 62-71

WARDLE, P. 1978: Regeneration status of some New Zealand confiers, with particular reference to Libocedrus bidwillii in Westland National Park. N.Z. Journal of Botany 16 : 471-7.

_____ 1979: Forest and climatic change - the status of the 'Holloway Theory'. Royal N.Z. Institute of Horticulture Annual Journal 7 : 133-44.

_____ 1980a: Ecology and distribution of silver beech (Nothofagus menziesii) in the Paringa district, South Westland, New Zealand. N.Z. Journal of Ecology 3 : 23-36.

_____ 1980b: Primary succession in Westland National Park and its vicinity, New Zealand. N.Z. Journal of Botany 18: 221-232

_____ 1980c: Floristic notes for the region between the Taramakau River and Haast River, Westland, New Zealand. N.Z. Journal of Botany 18 : 53-60.

_____; MARK, A.F. 1956: Vegetation and climate in the Dunedin District. Transactions of the Royal Society of N.Z. 84 : 33-44.

_____; McKELLAR, M.H. 1978: Nothofagus menziesii leaves dated at 7 490 yr B.P. in till-like sediments at Milford Sound, New Zealand. N.Z. Journal of Botany 16 : 153-7.

WATT, A.S. 1947: Pattern and process in the plant community. Journal of Ecology 35 : 1-22

WHITE, P.S. 1979: Pattern, process, and natural disturbance in vegetation. The Botanical Review 45 : 229-299

WHITMORE, T.C. 1974: Change with time and the role of cyclones in tropical rain forest on Kolombangara, Solomon Islands. Commonwealth Forestry Institute Paper No.46, Oxford, 92 pp.

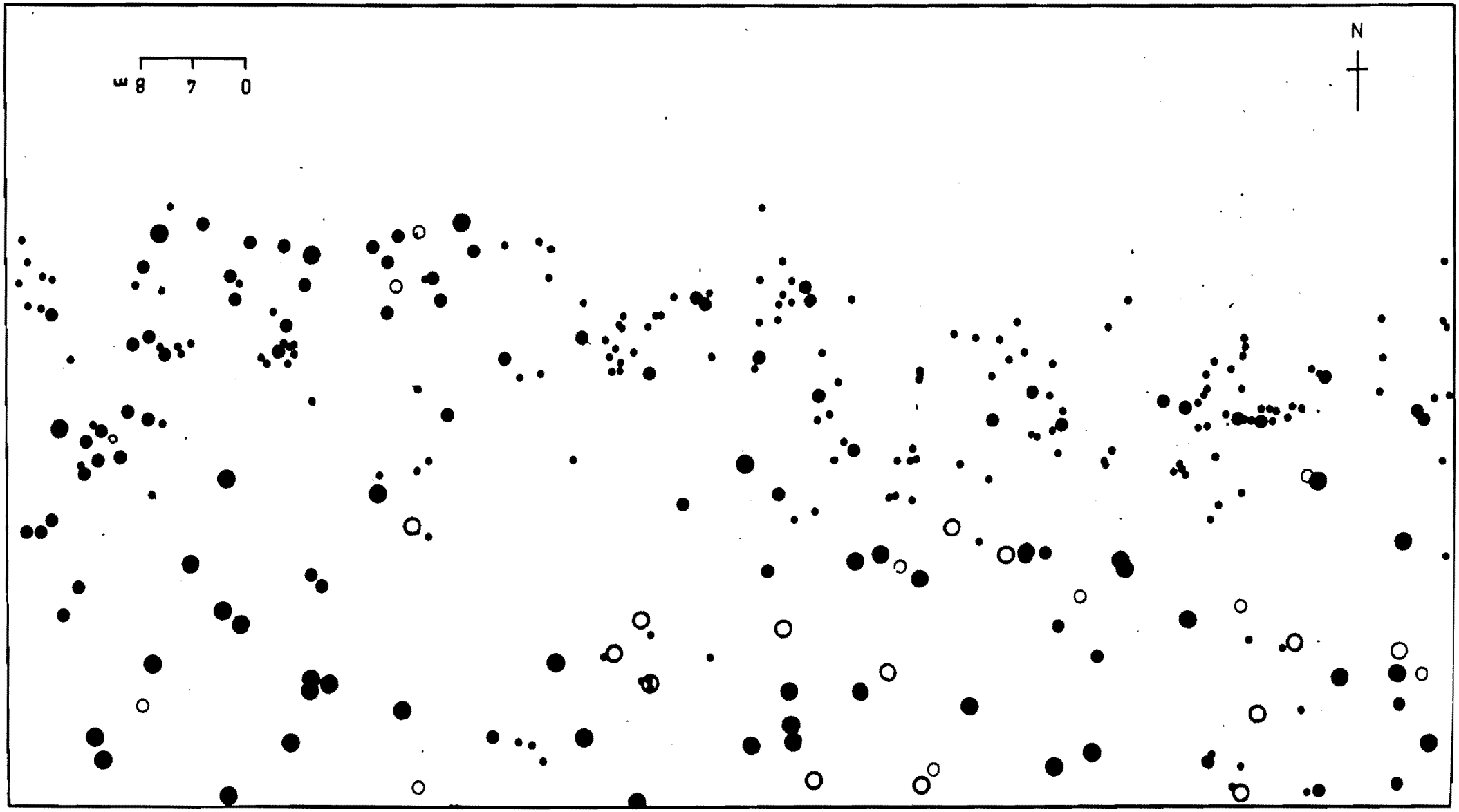
_____ 1975: Tropical Rain Forests of the Far East. Clarendon Press, Oxford, 282 pp.

WILLETT, R.W. 1950: The New Zealand Pleistocene snow line, climatic conditions and suggested biological effects. N.Z. Journal of Science and Technology B32 : 18-48.

WILSON, A.T.; HENDY, C.H.; REYNOLDS, C.P. 1979: Short-term climate change and New Zealand temperatures during the last millenium. Nature 279 : 315-7.

ZOTOV, V.D. 1938: Some correlations between vegetation and climate in New Zealand. N.Z. Journal of Science and Technology 19 : 474-87.

_____; ELDER, N.L.; BEDDIE, A.D.; SAINSBURY, G.O.K.; HODGSON, E.A. 1938: An outline of the vegetation and flora of the Tararua mountains. Transactions and Proceedings of the Royal Society of N.Z. 68 : 259-324.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APPENDIX I A section of the beech forest boundary

A permanent plot was established in Stand 3C in 1975 for the long-term monitering of population dynamics (section 3.11). The plot covers a section of the beech forest boundary and adjoining beech forest which is comprised of Nothofagus truncata. It is located at map reference NZMS1 S45/1149922.

The positions of all N. truncata individuals taller than 2m within the plot are shown in the figure opposite. The smallest circles refer to individuals taller than 2m and up to 21cm in stem circumference at chest height, the medium-sized circles to individuals in the 22 to 125 cm circumference range and the largest circles to trees larger than 125 cm in circumference. Open circles represent dead trees.

The mapping was carried out using parallel 60m long transects located 15 m apart. Tape measures were laid out on the ground along the transects. A vertical projection from the transect to each individual was made using a sighting device (see section 3.9). Then the length of the projection and its position on the transect were estimated with tape measures to the nearest 0.1m. Stem circumferences were measured by placing a tape measure around each stem.

APPENDIX II

A MAJOR RANGE EXTENSION FOR HARD BEECH (*NOTHOFAGUS TRUNCATA*) IN THE SOUTH ISLAND (NOTE)

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ABSTRACT

The presence of hard beech (*Nothofagus truncata*) is recorded in South Westland.

Hard beech (*Nothofagus truncata*) has been found recently at five localities near the Arawata and Waiatoto Rivers, South Westland. The previously known southern limit for the species was a small, isolated stand at Blackwater Creek near Kumara (map reference NZMS1 S50 & 51 775698) which is 260 km to the north of the South Westland localities. This stand is an outlier to an extensive area of distribution in the North Westland-Nelson region (Hinds and Reid 1957). Holloway (1954) recorded the other three species of *Nothofagus* in South Westland, but did not mention hard beech.

The locations and details of the stands are shown in Table 1 and Figure 1. Further finds may be anticipated at similar sites, for example, on Gill Hill north of the Waiatoto River.

Table 1. HARD BEECH STANDS IN SOUTH WESTLAND.

Stand No. (see Fig. 1)	Location	Map reference (NZMS1 S97)	Extent
1	Nisson Hill	634 954	5 ha
2	Mount McLean	578 933	several trees
3	MacFarlane Mound	572 917	1 ha
4	Arawata	545 914	0.1 ha
5	Arawata Bridge	564 903	single tree

A collection of adult leaves demonstrated the presence of hybrid (presumed *N. truncata* x *solandri* var. *cliffortoides*) as well as pure forms in each stand. The single tree near the Arawata Bridge was a hybrid. Specimens have been deposited at the Botany Division, Department of Scientific and Industrial Research Herbarium (CHR).

All stands occur on low hills adjoining or protruding from the low-lying coastal plain, chiefly on north and west facing slopes, and within an altitudinal range of 30 m to 90 m a.s.l.

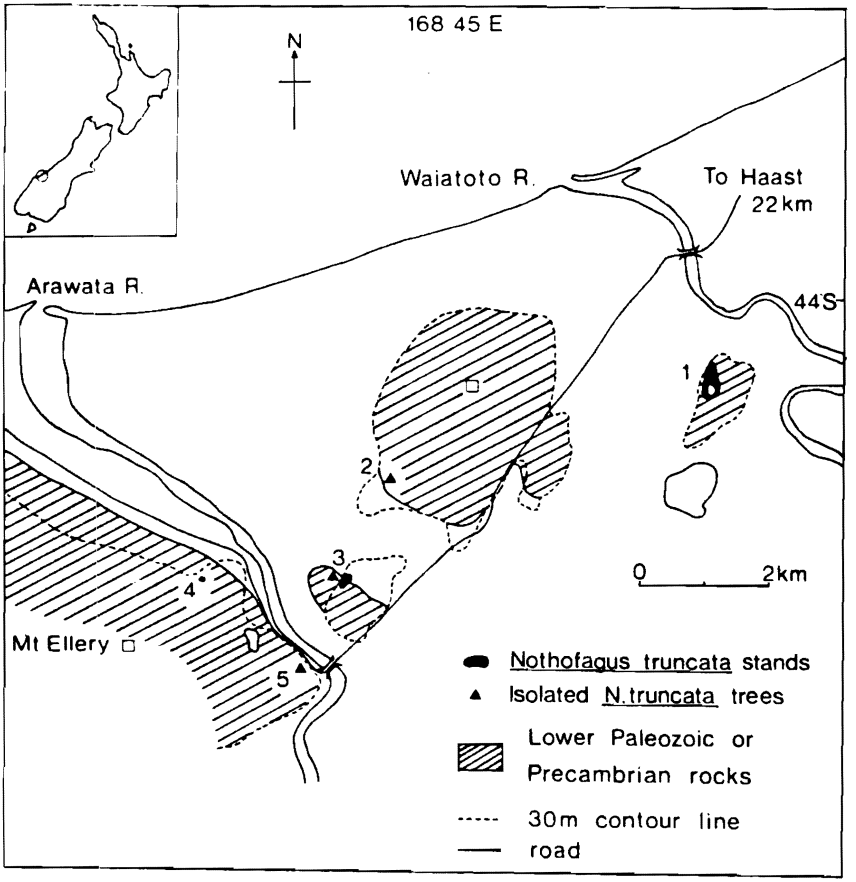

Fig. 1. Localities for *Nothofagus truncata* in South Westland, New Zealand.

In each case, the parent material is mapped as Lower Paleozoic or Precambrian rock (Mutch and McKellar 1964). Soils are shallow, well-drained and appear strongly leached.

The forest communities associated with hard beech range from tall forest where *Dacrydium cupressinum, Metrosideros umbellata, Nothofagus menziessi, N. solandri* var. *cliffortoides* and *N. truncata* are codominant, to low forest with *M. umbellata, D. colensoi. D. intermedium, N. solandri* var. *cliffortoides* and *N. truncata* codominant.

Extensive glaciation, temperature depression and the slow migration rates of *Nothofagus* have been held responsible for the absence of *Nothofagus* in much of south Westland (Willett 1950). Although the coastal plain between the Arawata and Waiatoto Rivers is mapped as being covered by a continuous ice sheet during the Otiran Glaciation (N.Z. Geological Survey, 1973) the present distribution of *Nothofagus* forest indicates that forest

vegetation was able to survive the glacial period within the area. The hard beech stands, therefore, point to the location of a number of vegetation refugia where trees and other plants could have escaped the influence of the ice cover.

ACKNOWLEDGEMENT

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LITERATURE CITED

HINDS, H.V. and REID, J.S. 1957. Forest trees and timbers of New Zealand. *New Zealand Forest Service Bulletin No. 12.* 207 pp.

HOLLOWAY, J.T. 1954. Forests and climate in the South Island of New Zealand. *Transactions of the Royal Society of New Zealand 82*: 329-410.

MUTCH, A.R. and McKELLAR, I.C. 1964. *Sheet 19. Haast. Geological Map of New Zealand 1: 250 000.* D.S.I.R., Wellington.

NEW ZEALAND GEOLOGICAL SURVEY. 1973. *Miscellaneous Series Map 6. Quaternary Geology - South Island.* D.S.I.R., Wellington.

N.Z.M.S. 1 S50 and S51 *Hokitika New Zealand Topographical Map 1: 63 360.* Department of Lands and Survey, Wellington.

WILLET, R.W. 1950. The New Zealand Pleistocene snow line, climatic conditions and suggested biological effects. *New Zealand Journal of Science and Technology Series B 32*: 18-48.

APPENDIX III Corrected radiocarbon dates

Radiocarbon dates based on the 'new' ^{14}C half life (5 730) years) and dates corrected for secular effects are described below for important events in the north Westland fossil record (Moar, 1971).

N.Z. Record No.	Location	Old $T_{\frac{1}{2}}$	New $T_{\frac{1}{2}}$	Secular
NZ 741	Crooked Mary Ck, Upper Grey Valley	6080 ± 100	6260 ± 110	6960 ± 130
NZ 830	Nan's Kettle, Bell Hill	2390 ± 50	2460 ± 60	2520 ± 60
NZ 1077	Tophouse	7830 ± 120	8060 ± 130	
NZ 1078	Ure's Mire, Upper Maruia Valley	6530 ± 85	6720 ± 100	

Corrected dates were provided by the N.Z. Geological Survey, D.S.I.R., Lower Hutt (E.M. Tiller and N.T. Moar, pers. comm.).

APPENDIX IV Summary of data on small seedling establishment, mortality and outgrowth in permanent quadrats. (Numbers of newly established seedlings are shown in brackets).

	Stand No.	Year of Observation			
		1974	1975	1976	1977
RIMU					
Total No.	3A	39	66 (32)	69 (20)	52 (2)
	3B	-	41	47 (16)	32 (1)
	3C	31	29 (3)	37 (9)	32 (2)
	5	18	22 (3)	20 (0)	23 (5)
	4A	-	48	62 (21)	57 (5)
	4B	-	10	16 (6)	12 (2)
No. Deaths	3A	-	6	17	11
	3B	-	-	9	14
	3C	-	2	2	6
	5	-	0	1	2
	4A	-	-	7	8
	4B	-	-	0	4
No. Outgrowing (Net)	3A	-	-1	0	7
	3B	-	-	1	2
	3C	-	3	-1	0
	5	-	-1	1	0
	4A	-	-	0	2
	4B	-	-	0	2
RATA					
Total No.	3A	4	5 (0)	5 (2)	6 (0)
	3B	-	3	5 (2)	4 (0)
	3C	52	54 (4)	64 (14)	61 (0)
	5	1	1 (0)	1 (0)	0 (0)
	4A	-	1	1 (0)	1 (0)
	4B	-	4	5 (1)	4 (0)
No. Deaths	3A	-	0	0	0
	3B	-	-	0	1
	3C	-	1	2	4
	5	-	0	0	0
	4A	-	-	0	0
	4B	-	-	0	1
No. Outgrowing (Net)	3A	-	-1	2	-1
	3B	-	-	0	0
	3C	-	1	1	0
	5	-	0	0	0
	4A	-	-	0	0
	4B	-	-	0	0

	Stand No.	Year of Observation			
		1974	1975	1976	1977
MIRO					
Total No.	3A	6	4 (0)	4 (1)	3 (1)
	3B	-	2	2 (0)	2 (0)
	3C	0	0 (0)	0 (0)	0 (0)
	5	1	3 (0)	3 (2)	0 (0)
	4A	-	8	8 (2)	4 (1)
	4B	-	7	4 (2)	5 (1)
No. Deaths	3A	-	0	1	1
	3B	-	-	0	0
	3C	-	0	0	0
	5	-	0	0	1
	4A	-	-	1	4
	4B	-	-	1	1
No. Outgrowing (Net)	3A	-	2	0	1
	3B	-	-	0	0
	3C	-	0	0	0
	5	-	0	0	0
	4A	-	-	1	1
	4B	-	-	4	-1
HARD BEECH					
Total No.	3A	100	86 (0)	87 (19)	123 (62)
	3B	-	29	28 (7)	101 (74)
	3C	64	49 (0)	38 (2)	57 (30)
	4A	-	146	145 (43)	163 (54)
No. Deaths	3A	-	9	8	16
	3B	-	-	5	1
	3C	-	10	9	9
	4A	-	-	14	18
No. Outgrowing (Net)	3A	-	5	10	10
	3B	-	-	3	0
	3C	-	5	4	2
	4A	-	-	30	18
RED BEECH					
Total No.	5	29	23 (1)	22 (2)	33 (18)
	4B	-	29	17 (4)	40 (27)
No. Deaths	5	-	4	1	8
	4B	-	-	12	3
No. Outgrowing (Net)	5	-	3	2	-1
	4B	-	-	4	1

APPENDIX V . Vegetation of an old burn site, Price's Creek

Location

A north facing ridge leading to Callaghans Creek; map reference NZMS 1 S45:037951; to the north of Stand 2 (Table 4). The area of the old burn is approximately 250m × 550m.

Stand history

A formed, graded track dating from the goldmining era of the last century passes along the ridge. The area has been fired, presumably repeatedly.

Vegetation

A low shrub vegetation less than 3 m in height. Rimu saplings and poles, gorse (Ulex europaeus), Carpodetus serrata, Cyathodes fasciculata and Pteridium aquilinum are the major species. Scattered Leptospermum scoparium, Pseudopanax crassifolium, Coprosma rugosa, Metrosideros umbellata, Weinmannia racemosa and Quintinia acutifolia are also present, together with a moderate density of large miro seedlings and rare kahikatea seedlings. The remains of trees of the original forest are well decayed. Undisturbed podocarp-hardwood forest occurs on all margins.

The rimu seedlings and saplings (greater than 40 cm tall) are present at densities of about 900-1000 ha^{-1}.

A sample of nine aged individuals showed that most were around 20 years of age and the oldest was 30 years old. The tallest sapling was 5.5 m tall.

APPENDIX VI Data for growth ring widths in rimu stem sections, showing the width of each successive group of 10 rings to the nearest 0.5mm, beginning at the centre of the stem.

STAND 1 (Callaghans)

Tree No.											
1	1	1.5	2	2.5	2.5	3	3	2	6	7.5	7
	2	2.5	2.5	2	2	2	2	6	7	8	9
	10	12	13	10.5	9	8.5	9	12.5	13	15	20
	12	11									
2	2	2	2.5	2	2	2.5	3	2	2	3	2
	3.5	3.5	3	2.5	2	4	3	3	2.5	3	2
	3.5	2	3.5	1.5	1.5	1.5	1.5	1.5	2	4	
3	1	2	5	21	8	7	8	8	7	7	10
	9.5	12.5	8.5	13	19	21	19	18	18.5	24	19.5
	22	19	16	19	17	20.5	12	14.5	14	10.5	10.5
	8.5	14	11.5	9	9.5	7.5	5.5	4	4	4	
4	1	2	2.5	3	3	2.5	2.5	2.5	4.5	3.5	2.5
	2	3.5	4	3	2.5	3	3	3	3	2	1.5
	2	1.5	2.5	2.5	4	5					
5	1	1.5	1	1.5	2	3	3	3	5	4.5	3.5
	3	4	3.5	2	3	3	2.5	4	4.5	4	4
	5	4.5	4	5	4.5	3	4	6	7	7.5	8.5
	5.5	8.5	9.5	9.5	7	6.5	7.5	10	10	10.5	9
	14	11	13	11	10.5	15.5	9	4.5	7	5	5.5
	5	5.5	9	11	6	12					
6	2	3	1.5	1.5	1.5	1.5	1.5	1.5	2	1.5	4
	4	5.5	4	2	3	3.5	2.5	1.5	1.5	3	3
	3	5	9.5	9.5	6.5	6.5	5.5	5.5	3.5	4	7.5
	8	4.5	4	3.5	8	8	5	4.5	4	6	7
	6.5	12.5	8	5	4.5	2.5	2.5	5.5	5	5	
7	2.5	2	2	2.5	3	2	1.5	2	4	3.5	7
	6	10	15	5.5	5	7	3.5	3.5	9	8.5	4.5
	3	3	7.5	2.5	3	3	3	3.5	4	5	5
	7.5	5	9	14	8	5.5	8.5	17.5	10.5	7.5	8
	2	2	2.5								
8	2	1.5	1	1	1	1	3	1.5	1.5	2.5	2
	4	5	4.5	2.5	1	2.5	4	5	6	6	6.5
	7	6	12	9.5	10	11.5	10	9	7	6	7.5
	8	10.5	6.5	3	3	4.5	3.5	3	2.5	3	3
	3.5	2	3	4	6.5	9.5	7.5	6.5	4.5	3	3
	2.5	3	2	2	3	7	9	9	3		
9	0.5	0.5	2	2	1	1	2	2	1.5	2.5	2
	4.5	1.5	2	3.5	3	3	4	6	4	6.5	7
	5	6	9.5	10	9	9.5	5.5	5.5	3.5	5	4.5
	5	9	10	11.5	11.5	8	9.5	9.5			

10	1	1.5	1.5	1.5	1	2.5	3.5	3	2.5	2	5
	7.5	5	4.5	8	6.5	5	5	6	4.5	2	3
	3	3.5	3.5	4.5	5	5	5	8	10	11.5	6.5
	5.5	7	11.5	7.5	10	10	11	9	5.5	4.5	5
	4.5	11	8	3.5	4	5	7.5	11	6.5	3.5	2.5
	2	1	1	2	3.5	3	2	2	2.5	4.5	4
	4	4.5	4	5	8						
11	2	1.5	1	1.5	3	3	2.5	1.5	4	5	5
	7	7.5	8.5	8	10	8.5	11	14	8.5	7	7
	5.5	7	7.5	7.5	7	4.5	5.5	4.5	7.5	9.5	11
	14	4									
12	1	2	2	2.5	2	4	2.5	2.5	5	7.5	5
	3	2	3.5	5	4	5	6.5	5.5	7	7	9.5
	9	5	6	5	7	8.5	8	12	12	10.5	13
13	1.5	2	3	2	1.5	1	1.5	1.5	3.5	3	5
	6	6	5	6	4	3	4	6.5	6	4.5	3.5
	5.5	4	9	8.5	6	8	9.5	8.5	7.5	7.5	10
	8	7.5	5.5	7.5	7.5	10	6	6	10.5	12	12.5
	11	10	8.5	10.5	9	8	8	9.5	10.5	7	3
	1.5	2.5	3	3	3.5	6.5	7	7	10		
14	2.5	2.5	3.5	3.5	4	4	5	7	4.5	4	5.5
	4	5.5	5	6	9.5	10.5	15.5	15.5	12	11	7.5
	6	7	7	9	6.5	6.5	9.5	9	14	14.5	9.5
	7.5										
15	3	2	1.5	1.5	2.5	3	6	5	5	2.5	2
	1.5	2	2	4	3.5	3.5	2.5	3	6	7	7
	8.5	13	11	20	21	22.5	17	17.5	18.5	16	15
	17	14	21	13	13	8	8	10.5	7	7	9
	7	8	7	5	7	6	5	3	3	4	5.5
	5.5	7	6	4.5	3.5	6	4	2.5	2	2.5	3
	2	3	3	2	2.5	2	1.5	2	2	2	2
	2.5	2.5	2	3	4	4					
16	2	1	1	2.5	2	1	1	2	2.5	2	3
	3	2	2	2	4.5	2.5	8	16	10	8.5	8
	7.5	10	10	11.5	14	11	17.5	11.5	8	10	16
	6.5	4	4	6.5	8	7	5.5	8	11	11	16
	17	12	10	6	8.5	21	19	18	9	11	8
17	2	1	2	2	2	2	3	3	8	6	7
	13	9	8	7	14	14	13	5	5	8	7
	5	4	3	2	2	6	8	12	10	11	10
	10	9	6	10	12	9	7	8	7	7	9
	9	14	14	11	5	2	5	5	4	4	18
	18										
18	2	2	2	1	1	5	4	3	3	2	5
	3	5	4	11	5	6	14	15	10	8	9
	8	18	13	11	8	6	6	5	6	5	10
	12	15	7	2	3	3	3	4	5	3	5
	4	4	4	5	4	5	7	9	11	4	11
	12										

19	1	2	3	3	2.5	1.5	5.5	6	2	2
	1	2	2	2	3.5	2	3	3.5	3	3
	3.5	3.5	4	9	8.5	9	4	2.5	6	7.5
	6	4	4	4	4.5	6	6.5	7	7.5	10
	7	6.5	8	6	5	4	4	5.5	5	5
	6	9	4	6	4.5	6.5	9	6	8	5
	5.5	4	5	9	10					
20	2	3	3	2	2.5	4	6	6.5	4	4
	3.5	11	9.5	8	7.5	7.5	9	12	10	7.5
	7	8.5	9.5	11	11.5	11	11	9.5	5.5	5.5
	5.5	6	4.5	4.5	3.5	3.5	4	4	4	6
	4	4.5	3.5	4.5	4	7.5	9	12	11	14
	17									
21	4	4	3	3	3.5	3	7	11	9	9.5
	9	9	16	15	14.5	11	15.5	21	10	9
	7.5	9	9.5	8	5.5	6	10	9	6.5	6.5
	10	8	4.5	4	5	4.5	5.5	6	6.5	6.5
	10	20	21	14	9	20.5	41	17	15	14
22	1.5	1	1	1	1	1	2	2.5	4.5	2
	3.5	4	4	3	4	5.5	7.5	8.5	7	3.5
	4.5	3	2.5	1	1.5	1.5	3	4.5	4.5	3.5
	3.5	4	4	3	4	5	4.5	4	5	7.5
	10	9.5	7	8.5						
23	2.5	3.5	4	4	4	4.5	3.5	5	3	5
	4.5	4.5	6.5	7	6.5	6.5	5	4	5.5	6.5
	8	6	4	2.5	7.5	10	12	10.5	7	8
	5.5	5.5	9	8.5	11	2.5	3	7.5	4.5	8
	10:5	8	10	6	3.5	3	2.5	3.5	3	3.5
	2	2	2	2.5	5					
24	1.5	1.5	1	2	2	2	3.5	2	2	2.5
	2.5	4	4	6	7.5	5	8	7	8	6.5
	6	9	8.5	7	10	9.5	10.5	12	16	14
	12.5	9.5	9.5	12	13.5	14	14	11.5	12	12
	10.5	13	15	14.5						
25	1.5	1.5	1.5	1.5	2	2	1.5	1.5	2	2.5
	1.5	2.5	2	4.5	2.5	1.5	2	4	4.5	4.5
	4.5	4	8.5	7.5	6.5	5.5	5	6	5.5	4.5
	5	4	5.5	9.5	7.5	7	4	7	10	10
	7	7	9							
26	0.5	2	1.5	2	1.5	2.5	1	1.5	3	4
	3	5	6	9	7	10.5	15	13	12	6.5
	11	9	15	8.5	13	7.5	8	6	4.5	4.5
	4.5	5	5.5	5.5	1.5	4	3	2	2	3
	1.5	2	2	4	3.5	2	1.5	1.5	2	2
	1.5	2	4	4.5	2.5	2	2	2	3	2.5
	2.5	2	2.5	3	4	3.5	6			
27	0.5	0.5	1	1.5	1	1.5	2	2.5	5	4
	5.5	4.5	9	15	10.5	8	10.5	11	14	15
	12	15.5	11	10.5	11	13.5	14	20	13	6
	4	10	13	17.5	14	12	14.5	21	8.5	7
	5.5	11.5	8.5	4.5	4					

28	2	2	2	4	4.5	5.5	6.5	4	5.5	5.5
	5.5	7	5	5	4	3	4	7	6	5.5
	6	10	10	8	8.5	6.5	5.5	5.5	8	7.5
	5.5	6.5	8.5	5	7	7	5	6.5	8	4.5
	5	5	5	4	6	6	6.5	4.5	4.5	4.5
	3.5	5.5	6	5.5	4.5	2	1.5	1.5	2	3
	2.5	2.5	1.5	1	1.5	1.5	2	2	2	2,
	2									
29	3	4.5	3.5	3	4.5	3	3	2.5	2.5	2.5
	3	4.5	6	7.5	9.5	7	7	7.5	10.5	10.5
	6	6.5	8.5	9.5	5.5	8	6	7	5.5	5.5
	6.5	7.5	7	7	4.5	4	4.5	5.5	3.5	4
	2.5	2.5	3.5	3.5	2.5	4.5	4	4	6	6
	4	4.5	4.5	4	2.5	3.5	3	4		
30	1	1.5	1.5	1	1	1	1	1	1.5	2.5
	3.5	3	3.5	2.5	3.5	3.5	3	2.5	3	2
	3.5	4	4.5	3	3.5	6	6	4.5	5	5.5
	7.5	4.5	5.5	7	7.5	9	10	11.5	7	11
	6.5	8	9.5	6	4.5	6	10.5	11	8.5	6.5
	8	7	6	10.5	10	7	5	5.5	8	9.5
	10	9.5	8	8.5	7	5	3	2.5	3.5	4.5
	5	5	4	1	1.5	1	1	1.5	1	1
	1	1								
31	3.5	3	3.5	5.5	4	4	4	3	3.5	6
	8.5	8	5.5	6.5	13.5	10.5	11	10	8	12
	13.5	9.5	8	10.5	12	13.5	15	10.5	12	8
	11	10.5	7.5	6	12	9	5.5	8.5	13	10.5
	5.5	4.5	7	5.5	7	11.5	12	10.5	12	10
	3	5	8	5.5	5	4	4	3	3.5	5.5
32	1.5	1	1.5	1	1.5	1	2	2.5	3	3.5
	4.5	4	4	5.5	7	8	5	5	5	8.5
	11	5.5	6.5	9.5	9.5	8	8	4.5	11.5	15.5
	14.5	12.5	10.5	7.5	7	7.5	10	14	18	14.5
	16.5	10.5	10	15	16	12	7.5	5.5	4	2.5
	3	14	11	11						
33	1	1	1.5	1	1	2	3.5	5	6	3.5
	3	4.5	6	4.5	6	5	7.5	11	12	12
	13	12.5	11	11.5	10.5	12	15.5	12	15	12
	10.5	18	15	18	16	16	14	10	16	14.5
	19	15	10	10	7.5	12	14	11.5	9.5	9
	10	4								
34	1	1	1	1.5	1	1.5	1.5	2.5	1.5	2
	2.5	1.5	3	4	5.5	7	9.5	8.5	10	7.5
	10.5	15	12.5	10.5	10	10	10	11.5	10	12
	14	14.5	10.5	10.5	11	12	9	8	11	18
	12	10	10.5	11	11	11	13			
35	1	1.5	3.5	1.5	2	2	2	2.5	4	5
	4.5	3.5	4	4	4	6.5	6	8.5	10	7
	5	7.5	6	6.5	7	6	5	7.5	9.5	6.5
	5.5	4	4	5	8.5	6.5	5	7.5	6.5	5
	7.5	10.5	11.5	11.5	7	4	3	4.5	5	5
	7	5.5	4							

36	2	2.5	2	1.5	3.5	2	5	2	2.5	1.5
	7.5	6	5	3	5.5	6.5	6.5	7	8	8.5
	9	9.5	11.5	10	8	7.5	8	7	6	9
	9.5	4	4.5	6	8.5	6	9	9	8.5	4
	4	2.5	4	4	2.5	4.5	2	2	2.5	3.5
	4	4	3	3.5	3	4.5	3	2	2	2.5
	2.5	2	2							
37	2	2	2.5	2.5	3	1.5	2	1.5	1.5	2
	2	2	2.5	1.5	1.5	2	3	2.5	4.5	4
	2	2.5	3	2.5	2.5	7	6	11	9	6
	7.5	12	9.5	11.5	13	13	9	14	11.5	13
	15	11	7.5	10.5	8	11	10	7	6	3.5
	4.5	4	4	4	3.5	3	3.5	5	6	4
	2	1.5	3	2	3	2.5	2.5	1	2	2
	2	1.5	1.5	1.5	2	2	2	2		
38	1.5	3	1.5	1.5	1	2.5	3	1	1.5	2
	1.5	2.5	5.5	2.5	2.5	2	1	2	2.5	3.5
	5.5	2	3.5	4.5	10	13	8	9	4.5	4
	6.5	12	8.5	7.5	5	5	6	3.5	5.5	4
	4	4	3.5	3.5	3	3.5	2.5	2.5	2	2.5
	2	4	5	3	1.5	2.5	4.5	2.5	4	5.5
	4.5	7.5	6	4.5	4	3	3	3	4	3.5
	4	4	4.5	4	5	5	4.5	9	9	6
	3.5	2	2.5	2	3	4.5	7.5	6		
39	1	1	1	1.5	2	3	1.5	2	5	3.5
	3	3	2.5	7	2	4	3	4	2.5	3.5
	4	4	4	4	6.5	10.5	3.5	3	3	2
	1.5	2.5	2.5	4	3.5	2.5	2	2	2	3
	2.5	3	4.5	4	5	4.5	7	6.5	4.5	5
	5	8	8.5	8.5	7.5	8	8	7	6.5	7
	8	10.5	11.5	11.5	13	13.5	8	7	6.5	7
	7.5	9	7	8	9	8.5	7.5	6.5	7.5	7.5
	6.5	7	5	5	5	5	6	4.5	4.5	6
	8.5	7	6.5	4	5	3.5	3.5	3	3	3
	4	2.5	3	3	3.5	4	5	5	4	3
	3	3	3	2.5	3	2.5				
40	1	1.5	1.5	1.5	2	1	2	2	3	1.5
	2	1.5	2.5	3.5	3	4	3	4	8	6
	3.5	4.5	4	6	6	7	5	6.5	10.5	10.5
	8.5	6	8.5							
41	2	1	2	1.5	1	1.5	2.5	2	4	2
	2	6	4.5	5	5	6	6	3	4	3
	4	4	4.5	5	3	3	3	3.5	4	5
	4.5	4	4	4	5	4				
42	1	1	2	2	1.5	1.5	2	2	3	2.5
	2	2	2.5	2.5	2.5	4.5	2	3	6	5
	1.5	2	7	7	5.5	6				
43	2	2.5	2.5	2	2	2	2	2	1.5	2.5
	2	2	2.5	4.5	4	5	4	3.5	4	7
	6	6	4.5	3						

44	1.5	1	1	1.5	2	1.5	1.5	2	3	3.5
	2.5	6	5	4	5	6	6.5	4.5	4.5	2
	6									
45	1.5	2.5	1.5	2	3	1.5	1.5	1.5	1.5	2
	1.5	3	1.5	1.5	2	2	2	1.5	3	3
	6	3.5	4.5	3.5	4	4	4.5	2.5	3	4
	3	3	2.5	1.5	2.5					
46	0.5	0.5	1	1	0.5	1.5	1.5	3	1.5	1.5
	2	3.5	5							

STAND 6 (Notown)

48	1.5	2	1.5	1	2	2.5	3	2	3	2.5
	2	4	5.5	8	13	12	13.5	12	12	18
	23	17	11	8	9.5	8	7	10	12	8
	11	11	9	7	7.5	9	9	12	18	19
	16	12								
49	4	4	2.5	3.5	5.5	7	7	11	15	12
	20	18	20	19	20	23	24	17	14	14
	15	16	13	9	7	9	10	7	5	5
	5	7	3	4	3	9	6	5	6	5
	5	6	5	5	6	6	6	9	15	11
	7									
50	4	4	5	2	5	3	3	10	12	16
	18	13	15	18	19	25	18	13	15	17
	20	16	13	13	16	13	16	13	9	4
	4	8	9	8	6	6	8	13	15	8
	9	27								
51	4	4	5	2	5	3	3	10	12	16
	18	13	15	18	19	25	18	13	15	17
	20	16	13	13	16	13	16	13	9	4
	4	8	9	8	6	6	8	13	15	8
	9	27								
52	1	1	1	2.5	4	4	4.5	5.5	6	4.5
	5.5	4.5	3	7	12	8	11.5	9	4.5	5
	4	3	5	14.5						
53	1.5	1.5	1	1.5	1	1	2.5	2.5	2	2
	3	5.5	5.5	4.5	4	4	4	2	6	7
54	1	0.5	0.5	1	1	1.5	1.5	1	1	1
	1	1.5	1.5	1.5	1.5	1.5	2	2.5	3	3.5
	7.5	12	10.5	6	9	7	6	4.5	6.5	11
	11	18	10	6.5	5	6.5	5	4.5	9	5
	4	7	4	5	5	4	4.5	6	4.5	4.5
	6	4	6	5	4	3	2.5	4.5	4.5	5
	8	7.5	7.5	3	14	7	9	4	3	4.5

55	1	1	1.5	1.5	1.5	2	3	4.5	7	12.5
	10.5	11	14.5	18	18	18	11	12	7	4.5
	5	8	7.5	4.5	4.5	5.5	4	5	10.5	9
	5	4.5	5	5.5	5	4	4	3.5	4.5	3.5
	4	3.5	4	3.5	7.5	8	10	10.5	12	7.5
	6	5.5	4							
56	1	2	3	2.5	3.5	2	3	4	5	5.5
	5.5	7.5	7.5	11	11.5	9	10.5	9	8	6.5
	7	6	12	6	6	4.5	3	3	3	2.5
	4	3.5	4	5	5	3.5	3.5	3.5	4.5	4.5
	5.5	5	5.5	6.5	6	5.5	5.5	5.5	5	3
	3	3	5	5.5	6.5	4	7	6	5.5	7
	8	6	6.5	8	7	9	8	12	11	10
	11	10.5	12.5	14	10.5	6				
57	2	1.5	1.5	1.5	2.5	2.5	1.5	2	2.5	1.5
	2.5	0.5	1	0.5						
58	1	1	1.5	1	1.5	4.5	4	3	4.5	5.5
	3.5	3								
59	1	1.5	1	1.5	2	1.5	1	1.5	2	1.5
	1	3	4.5	2	2	2.5	2	2.5	1	1
	1	1	1.5	3.5	3.5	2	2	2	4	3.5
	3.5	3.5	3	5	4	7.5	7	6.5	7	7
	7.5	8	9.5	7.5	9.5	8.5	8	8	6.5	6.5
	6	4.5	4.5	5.5	4.5	3	2.5	2	3.5	4
	3									
60	1	3	4.5	7	10	10	7	5	5.5	5
	4	6	14	9	8.5	12.5	10.5	10	8.5	10.5
	9.5	5	4.5	4	4	6.5	6	4.5	7	8
	12	11	11	12	11	9	8.5	9.5	10	12.5
	7.5	9	8	8	8	7	6.5			
61	1.5	2	1.5	3.5	5	4.5	8	4.5	4.5	6.5
	5	4	6.5	8	6.5	7.5	9.5	10.5	6	14.5
	12.5	13	15	15.5	16.5	10	13	20	12	12.5
	8	8.5	8	8.5	11	11	12	12	16	12.5
	14.5	13.5	11	13	7.5	10	9	8	8.5	10
	6.5	8	5.5	4.5						
62	1	1	1.5	1	1	1.5	1	1	1	0.5
	1	2	4	5	4.5	4	5	4.5	4	3
	4.5	4	3	2	3	2.5	1.5	2	4.5	3
	3	4	4	5	11.5	11	9	8	9	8
	8.5	7.5	11	11.5	9.5	12	12	9	8	12
	10	5.5	5.5	4	5.5	6.5	5.5	3.5	3	4
	4	6	5	4.5	2	1.5	2	2	2	3
	4.5	4	3	2.5	1.5	1.5	1	1.5	1.5	1
	2	1.5	1.5	2	2	2	3.5	2.5	2	2
	2	1.5	1.5	2	2.5					

63	1	1	1	1	1	1	1.5	3	6	3
	3	2	2	1.5	1.5	3.5	12	10.5	10	9
	14	14	12.5	13	12	13	9	14	11.5	16
	14	13	15	12.5	12	11	12.5	12	10	4.5
	4	4.5	6	3	3.5	3.5	4.5			
64	1	1.5	4	10.5	7.5	4	3.5	2.5	4.5	14
	10	15	12	11.5	9.5	10	13	15.5	7.5	5.5
	4	5.5	5	6	5.5	6	8.5	8	6.5	7
	13	10	11	12.5	5	3.5	4.5	4.5	10	13
	12.5	11	17	23	13	11	11.5	11	10	9
	8	9	6	5	4	9	13.5	11	6.5	6
	10.5	9	13.5	9.5	5.5	5	5	5	4	3.5
	6	5								
65	1	1	1	1	1	1.5	2	1.5	2	1.5
	2	8	20	23	19	7	3	9	8.5	8.5
	10	6.5	7.5	7	12	10	16.5	16	12.5	7.5
	7	9.5	13	10	9	6.5	7.5	8.5	5	6
	4.5	4	4	5.5	5.5	4	5	9	8	5
	5	6	5	6	4.5	5	3	3.5	3	3
	4	3	4	3.5	3	4	3.5	4	3	2.5
	3	2	2.5	4	4.5	7	8	5	4.5	5
	8	8	10	8	6	8	8	6.5	6	8
	7	4	8	13.5	10.5	5	4.5	4.5	3	